ECOPHYSIOLOGY OF NORTHERN SPRUCE SPECIES

The performance of planted seedlings

Steven C. Grossnickle

Ecophysiology of Northern Spruce Species

The Performance of Planted Seedlings

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The Performance of Planted Seedlings

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Abstract

Seedling establishment and subsequent growth on a reforestation site are paramount to successful forest regeneration. Spruce seedling performance depends on both inherent seedling growth potential and the degree to which environmental conditions allow this growth potential to be expressed. This inherent growth potential of spruce seedlings is related to morphological and physiological characteristics. Therefore, it is the physiological response of spruce seedlings to site environmental conditions that ultimately determines seedling performance.

This book provides foresters with the necessary information to understand the performance of spruce seedlings after being planted on a reforestation site. It was written for an anticipated audience of university students who are taking a regeneration silviculture class, plus foresters and researchers who work with spruce species within forest regeneration programs throughout the world.

The book was designed so that the reader can develop an initial understanding of primary physiological processes of spruce seedlings and the importance of these processes when making silvicultural decisions. The scientific discipline of ecophysiology examines the physiological and morphological processes of plants in response to the surrounding environment. The primary focus of this book is the physiological processes of northern spruce species at the whole plant level in response to the surrounding environment. The following fundamental physiological processes are discussed: water relations, gas exchange, mineral nutrition, freezing tolerance, dormancy, and morphological development. Examples of how genetic variation can affect the ecophysiological response of spruce species are also presented. The book briefly examines major components of the seedling environment on reforestation sites and how these components influence seedling responses.

Understanding the ecophysiological performance capability of northern spruce species is a prerequisite for successful implementation of plantation forestry. With this knowledge, silviculturists will improve their capabilities to grow spruce seedlings within forest regeneration programs. The book covers all aspects of ecophysiological performance of northern spruce species in relation to currently used forest regeneration practices. It is intended to provide foresters with enough information on these processes to enable them to understand what type of effects their silvicultural decisions are having on subsequent seedling performance. Foresters will then be equipped to make knowledgeable silvicultural decisions as they implement their forest regeneration programs, thereby improving spruce seedling survival and growth.

Résumé

L'établissement de semis et leur croissance subséquente dans un site de reforestation jouent un rôle clé dans le succès de la reforestation. Le rendement des semis d'épinette dépend du potentiel de croissance inhérent des semis ainsi que des conditions environnementales qui permettent le développement du potentiel de croissance. Ce potentiel de croissance des semis d'épinette est associé à des caractéristiques morphologiques et physiologiques. C'est donc dire que la réaction physiologique des semis d'épinette aux conditions environnementales déterminent, en bout de course, le rendement des semis en question.

Ce livre a été rédigé afin d'offrir aux experts-forestiers l'information nécessaire pour comprendre le rendement des semis d'épinette après la plantation sur un site de reforestation. Il a été rédigé principalement à l'intention des étudiants d'université s'intéressant à la régénération des forêts ainsi qu'à l'intention des experts-forestiers et des spécialistes qui utilisent et étudient l'épinette dans des programmes de régénération des forêts du monde entier.

Cet ouvrage a été conçu de façon à ce que le lecteur puisse acquérir une connaissance de base des processus physiologiques primaires des semis d'épinette et de l'importance de ces processus dans la prise de décisions en sylviculture. La discipline de l'écophysiologie s'intéresse aux processus physiologiques et morphologiques des plantes selon leur milieu. L'auteur y explore les processus physiologiques des diverses espèces d'épinette dans leur environnement. On traite, dans ce livre, des processus physiologiques fondamentaux suivants : les relations avec l'eau, l'échange de gaz, la nutrition minérale, la tolérance au gel, le repos végétatif et le développement morphologique. On y présente également des exemples de la façon dont la variation génétique affecte la réaction écophysiologique des espèces d'épinette. On examine aussi brièvement les principaux éléments de l'environnement des semis dans les sites de reforestation et la façon dont ces éléments influencent la réaction des semis.

La compréhension de la capacité de rendement écophysiologique des espèces d'épinette est essentielle à l'implantation efficace dans le secteur de la sylviculture de plantation. Armés de cette compréhension, les experts-forestiers amélioreront l'efficacité de leurs plantations dans le cadre de programmes de régénération des forêts. Ce livre traite de tous les aspects du rendement écophysiologique des espèces d'épinette en relation avec les pratiques actuelles de régénération des forêts. Il vise à offrir aux experts-forestiers suffisamment d'information quant à ces procédés pour leur permettre de comprendre les effets de leurs décisions sur le rendement des semis. Les experts-forestiers pourront ainsi prendre des décisions éclairées en régénération de forêts, améliorant par le fait même le taux de survie et de croissance des semis d'épinette.

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List of Abbreviations

ABA	abscisic acid
ATP	adenosine triphosphate
DBB	days to budbreak
DBB_t	days to terminal budbreak
DWF	dry weight fraction
e_a	ambient vapor pressure
e_s	saturated water vapor pressure
g_{wv}	stomatal conductance
H	sensible heat flow
II	index of freezing inj[illegible]t a given temperature
LE	latent heat flux
LT_{50}	freezing temperature resulting in 50% needle electrolyte leakage
M	metabolic energy
N	number of measurements
p	probability level
PAR	photosynthetically active radiation
PGPR	plant growth promoting rhizobacteria
pH	concentration of hydrogen ions in a soil solution
P_n	net photosynthesis
Q_{10}	ratio of the respiration rate at temperature T to the rate of respiration at temperature $T - 10°C$
RGC	root growth capacity
R_n	net radiation
RWC	relative water content
RWC_{tlp}	relative water content at turgor loss point
S	heat storage
SPAC	soil–plant–air continuum
TR	transpiration rate
VPD	vapor pressure deficit
WUE	water use efficiency
$\delta^{13}C$	carbon isotope composition
Ψ	water potential
Ψ_{min}	minimum daytime shoot water potential
Ψ_p	turgor potential
Ψ_π	osmotic potential
Ψ_{pd}	predawn shoot water potential
Ψ_{sat}	osmotic potential at saturation
Ψ_{soil}	soil water potential
Ψ_{tlp}	osmotic potential at turgor loss point

Introduction

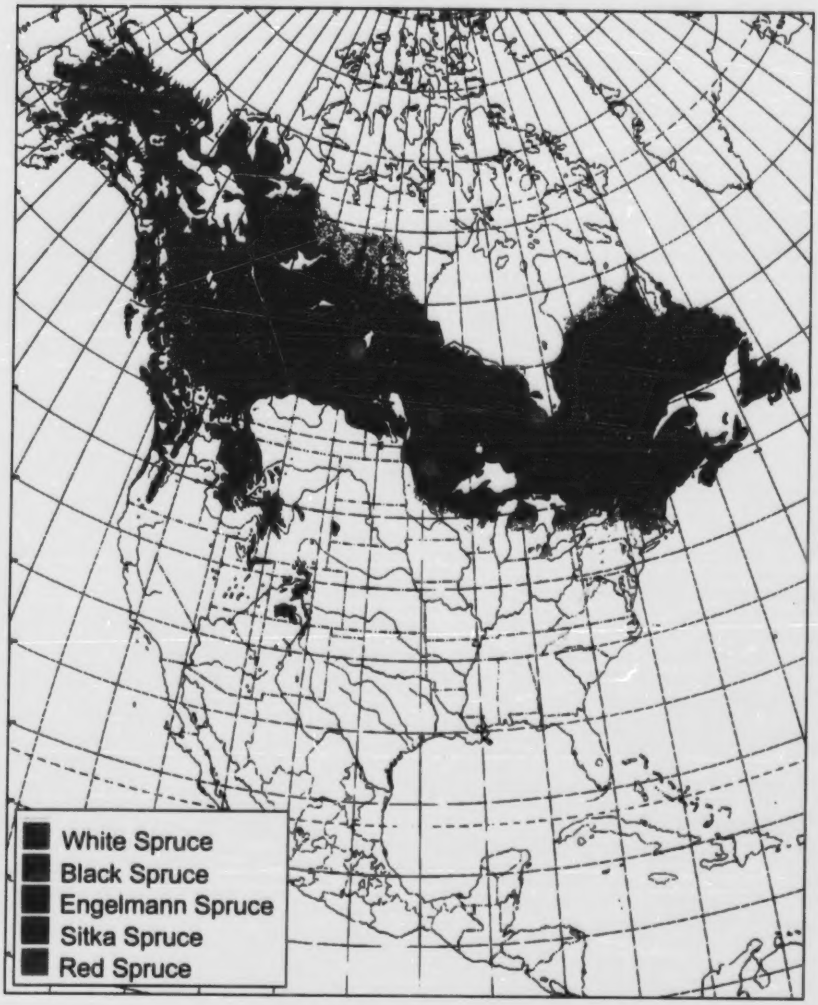
As society puts more pressure on the forested land base, there is an increasing call to preserve more of the remaining old-growth forests and forests of an ecologically sensitive nature. However, society still needs forest-based products to maintain current standards of living. If resources, such as forest-based products, can be produced in ways that reduce human pressures on biological diversity, then resource production zones (e.g., high-yield forest plantations) can have a positive overall effect on the conservation of biodiversity (Salwasser and Pfister 1994). To meet future demands for softwood fiber utilized for pulp and timber, forest productivity must increase within each given area, rather than by managing more forest area (Gladstone and Ledig 1990; Kimmins 1997; Spears 1998). To increase this timber productivity on a smaller land base (i.e., high-yield plantations), intensive silviculture practices need to be implemented (Sedjo 1999). If foresters are going to be successful in developing these high-yield forest plantations, they need to have a good understanding of how planted seedlings respond to applied silvicultural practices. This treatise is intended to provide foresters and researchers with a synthesis of available information on the ecophysiological performance of spruce (*Picea*) species planted in forest plantations throughout northern latitude forests of the world.

Spruce species are widely distributed in coniferous forests of the northern boreal and mountain, and temperate forest regions throughout the northern hemisphere. There are six spruce species that are of primary interest in world-wide silviculture programs. These include black spruce (*Picea mariana* (Mill.) B.S.P.), Engelmann spruce (*Picea engelmannii* Parry), Norway spruce (*Picea abies* (L.) Karst.), red spruce (*Picea rubens* Sarg.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.), and white spruce (*Picea glauca* (Moench Voss)). These spruce species cover the northern latitudes of the great land masses of North America, Europe, and Asia, where colder and wetter climates prevail, and only venture south in the mountainous regions of these continents.

Black spruce has a transcontinental distribution that spans North America and is one of the most widely distributed conifers in Canada. Black spruce occurs in the northeastern United States, through the northern Great Lakes and up around Hudson Bay, and west into the northeastern region of the province of British Columbia and up into Alaska, east of the coast mountain range (Fig. 1). This species is generally located within low- to mid-elevation forests below 1500 m.

Engelmann spruce is widely distributed in the western inland region of North America and is typically found in subalpine forests of the mountains that extend from Arizona and New Mexico in the United States, at the southern portions of this range, northwards into central Alberta and north central British Columbia (Fig. 1). This species has a wide elevational distribution from as low as 500 m in the north to high-elevation forests, above 3000 m, in the south. Within British Columbia, Engelmann spruce has a range that extends from east of the coast

Fig. 1. The geographic ranges of spruce species across North America (adapted from Burns and Honkala 1990).



mountains into the Rocky mountains and is generally found above 600 m in elevation.

Norway spruce is the most widely distributed spruce species on the European and Asian continents. There are three ranges identified for Norway spruce. First is central and southeastern Europe, primarily in the mountainous areas (i.e., the Alps, Carpathain, and Rhodope mountains) that extend southward through the continent. Second is northeastern Europe which includes the Scandinavian countries. Third is the Siberian range that extends through the boreal forests of western and central Russia. This species is found near sea level in the north and within high-elevation forests, above 1500 m, in the south. Norway spruce has also been used in forest plantations in Canada, northeastern United States, the United Kingdom, and Iceland.

Red spruce is regionally distributed in eastern North America and is typically found in forests of the Appalachian mountains that extend from Georgia in the United States, at the southern portions of its range, northwards into the northeastern United States, and north into the Atlantic Provinces of Canada (Fig. 1). This species is found near sea level in the north and within higher elevation forests, above 1500 m, in the south.

Sitka spruce is regionally distributed along the western coast of North America, west of the coast mountain range, from Alaska in the north, down through British Columbia to as far south as northern California (Fig. 1). This species is found near sea level in the north and within higher elevation forests, up to 1000 m, in the south. Sitka spruce has also been planted in the United Kingdom where it can be found in extensive plantation forestry programs.

White spruce has a transcontinental distribution. It spans North America and is one of the most widely distributed conifers in Canada. White spruce occurs in the northeastern United States, through the northern Great Lakes and into regions just below Hudson Bay, west into the northeastern region of the province of British Columbia, and northern Montana, and up into Alaska where it is generally found east of the coast mountain range (Fig. 1). This species is generally located within low- to mid-elevation forests below 1000 m.

White spruce and Engelmann spruce hybridize in geographic regions where their ranges overlap. In British Columbia, the extensive hybridization occurs at intermediate elevations of 600–1500 m (Dobbs 1976). Conventionally, white and Engelmann spruce and their hybrid are collectively called interior spruce. Forests dominated by interior spruce comprise approximately 23% of the forested lands within British Columbia (Coates et al. 1994).

Silviculture is the application of the knowledge of silvics in controlling the establishment, growth, composition, and quality of a forest (Daniel et al. 1979; Smith 1986). It utilizes an assortment of treatments to manipulate the vegetation and directs tree development to create or maintain desired conditions. The primary silvicultural treatments that foresters have to manage the forest include the following: selection of the harvesting system (also called silvicultural systems), site preparation, choice of species, regeneration approach (i.e., seed or seedling), fertilization, vegetation management, thinning, and pruning. Inherent within foresters applying good silvicultural practices is that they must have a thorough understanding of plant–environment interactions (Daniel et al. 1979). Incorporating an understanding of these interactions, along with proper silvicultural practices, allows foresters to apply this knowledge towards managing the establishment, growth, composition, and quality of forests to meet their defined objectives. Thus, it is a merging of biological knowledge of the forest species and site environmental conditions along with silvicultural treatments and economic considerations that should drive foresters when making their silvicultural decisions. One of the long-standing objectives of silviculture in North America is successful regeneration either by a natural process or by seeding or planting (Toumey 1916). Silvicultural practices can be very intensive during the initial stages of forest stand development. This is the primary period when foresters apply silvicultural treatments during forest development in the northern latitudes. In this treatise, the primary focus of the discussion is on the silvicultural treatments used to establish high-yield forest plantations of northern latitude spruce species.

During the initial stages of developing high-yield plantations, a series of intensive silviculture practices are required to ensure plantation success (Gladstone and Ledig 1990). First, a forester must choose the appropriate crop species. Second, tree improvement programs are required to improve the composite genotype of the crop species. Third, nursery culture must optimize the morphological and physiological conditions of seedlings prior to and at planting. Fourth, site modification may be required to improve the physical environment of the reforestation site to enhance the physiological performance and morphological development of the crop species. Understanding the ecophysiological capability of the crop species and how it performs in relation to forest regeneration practices provides foresters with a means to effectively apply intensive silvicultural practices to increase forest productivity. This treatise examines how northern latitude spruce species respond to these intensive silviculture practices that are required to ensure plantation success. In the following discussions, examples include silvicultural work from the United States, Europe, and the Scandinavian countries, although the major emphasis is primarily, but not exclusively, on silvicultural practices used throughout Canada.

Clear-cutting in its various forms is the most widely applied silvicultural system in use within plantation forestry programs throughout the world (Matthews 1989). The clear-cutting forest regeneration practice is defined as the removal of all trees from a forested stand followed by the regeneration of a new forest stand through seeding or the planting of nursery stock (Smith 1986). The practice of clear-cutting followed by planting is the recommended silvicultural system for use within the boreal spruce forests and the coastal Sitka spruce forests of Canada (Weetman and Vyse 1990). Although the use of other silvicultural systems for harvesting forests are on the rise in Canada, clear-cutting is still the dominant harvesting method used within the northern forests (87% of harvested lands were clear-cut in 1994). Within Canada, 816 353 ha of forests were harvested through the even-aged silvicultural system of clear-cutting in 1994 (Natural Resources Canada, Canadian Forest Service 1995). The clear-cutting silvicultural system is also the most commonly used regeneration method in the Scandinavian boreal forests containing Norway spruce and in the Sitka spruce plantations found in the United Kingdom (Matthews 1989; Weetman 1996). Clear-cutting is by far the most common silvicultural system used in spruce forests throughout the United States when timber production is the primary use of the forest land base. This harvesting approach, in conjunction with either natural seeding or the planting of seedlings, is considered the best silvicultural system for managing black spruce (Johnston and Smith 1983), eastern white and red spruce forests (Blum et al. 1983), Rocky mountain Engelmann spruce forests (Alexander and Engelby 1983), interior Alaska white spruce forests (Zasada and Argyle 1983), and coastal Sitka spruce forests (Scott 1980; Harris and Johnson 1983) found throughout the United States. The main attraction of clear-cutting as the silvicultural system of choice for plantation forestry operations is that not only is it a simple harvesting practice adapted to many site conditions, but also that it lends itself readily to technical innovations that are part of regeneration silvicultural practices (Matthews 1989). Discussions in this treatise focus on the performance of northern latitude spruce species in relation to the silvicultural practice of clear-cutting followed by the regeneration silvicultural practices that pertain to the planting of seedlings.

Recently, there has been much debate over whether to continue to use clear-cutting as the appropriate silvicultural system to harvest, regenerate, and tend northern latitude forests. Members of society have raised the question of whether there are alternative silvicultural approaches that can retain the forest structure while still allowing for the harvest of timber. Implementation of partial forest canopy retention systems may yield a number of benefits when trying to manage northern latitude forests of Canada (Lieffers et al. 1996*a*), Central Europe (Plochmann 1992), Scandinavian countries (Hansen et al. 1998), and the United States (Salwasser and Pfister 1994). Ecological benefits include the ability to sustain more ecosystem components thereby enhancing biodiversity and wildlife habitat, to sustain long-term nutrient cycling processes, to sustain long-term site productivity, and other aspects that are important in maintaining the integrity of a late-successional state of the forest ecosystem. Silvicultural benefits include increased yield from mixed species, the use of natural regeneration that may result in less intensive (i.e., costly) silviculture practices, improved connectivity of forest structure across the managed forest landscape, and more security of industrial forests on public lands through the use of silvicultural practices that maintain the forest structural integrity. Society needs to reconcile its desire to have high quality, and inexpensive, wood products with its desire to have the forests provide other cultural, social, and economic values. This treatise is not the forum for this forest management debate. Readers interested in a discussion on this topic are referred to a recently published treatise that examines new perspectives in forest ecosystem management (Kohm and Franklin 1997*a*). This treatise does include a section that discusses how silvicultural systems that provide partial forest canopy retention can influence the ecophysiological performance of planted spruce seedlings.

A number of alternative silvicultural system methods are now being used throughout the northern latitude forests on a very limited scale. One of these methods is the use of strip clear-cutting, primarily in black spruce forests

(Johnston and Smith 1983; Youngblood and Titus 1996). Group selection is another alternative silvicultural system used in mature black, white, and Norway spruce ecosystems (Johnston and Smith 1983; Zasada and Argyle 1983; Weetman 1996; Matthews 1989). Another silvicultural system that is being applied to northern latitude spruce forests is the shelterwood system. This silvicultural systems approach is now being applied on a limited basis to spruce-dominated forests throughout Canada (Weetman 1996; Younngblood and Titus 1996), the United States (Alexander and Engelby 1983; Blum et al. 1983; Harris and Johnson 1983; Johnston and Smith 1983; Zasada and Argyle 1983), and the European and Scandinavian countries (Matthews 1989). This treatise discusses the merits of these silvicultural systems, from an ecophysiological perspective, as alternatives to clear-cutting followed by the planting of seedlings within the northern latitude spruce forests.

Areas that were harvested within the northern latitude spruce forests are regenerated naturally, by seeding or the planting of seedlings. Over the past 10 years, areas that were regenerated by seeding or the planting of seedlings have averaged between 400 000 and 500 000 ha per year throughout Canada (Anonymous 1998). This equates to approximately 45% of the forests that were harvested during this time period (Anonymous 1995). The land base not seeded or planted is allowed to become reestablished through natural regeneration. Natural regeneration is the process of obtaining site reforestation using seed dispersed by forest on or adjacent to the site. This treatise does not discuss the regeneration of northern latitude forests through seeding, either by natural or as a direct silvicultural practice. This regeneration procedure is discussed in detail in a number of other sources, either as a general topic (Daniel et al. 1979; Smith 1986) or specifically for spruce species (Stiell 1976; Coates et al. 1994). A lack of successful forest regeneration can occur with broadcast seeding and natural regeneration because of inconsistent seedling establishment. Foresters who are mandated to successfully reforest harvested sites prefer to plant seedlings because it allows them to control species stocking and spacing, thereby ensuring that the application of intensive silviculture practices have the potential to successfully establish a young spruce stand on the site. This treatise discusses regeneration silviculture practices as it relates to the performance of planted seedlings.

Throughout the world, it is estimated that over one billion spruce seedlings were planted on a yearly basis during the 1990s (S. Grossnickle, personal survey). In the Scandinavian countries, Finland, Norway, and Sweden plant approximately 72 000 000, 20 000 000, and 195 000 000 Norway spruce seedlings, respectively, on an annual basis. Northern European countries such as Czechoslovakia and Germany plant approximately 125 000 000 and 50 000 000 Norway spruce seedlings, respectively, on an annual basis. In addition, other Northern European countries and Russia plant approximately 100 000 000 Norway spruce seedlings on an annual basis. The United Kingdom annually plants around 50 000 000 Sitka spruce seedlings into forest plantations. In the United States, approximately 20 000 000 Engelmann, white, black, and red spruce seedlings are planted every year. In Canada, a total 695 000 000 seedlings were planted in 1994. Of this total number of seedlings planted, approximately 436 000 000 were spruce seedlings. To implement reforestation programs with northern spruce species, a large forestry sector has been developed that deals with seedling production. Bare-root seedlings are the stocktype of choice for regeneration programs in the United Kingdom, the United States, and northern Europe. In Scandinavian countries, greater than 85% of all conifer seedlings are produced as container-grown seedlings (A. Mattsson, personal communication). In Canada, greater than 75% of all conifer seedlings are container-grown (Arnott 1992). Throughout the world, greater than 60% of all spruce seedlings are currently produced as container-grown seedlings. This trend is continuing with further increases in the use of container-grown spruce seedlings in plantation forestry programs. In this treatise, discussions on stock-type nursery culture as it relates to spruce seedling performance in the field and stock-type characterization prior to field planting are primarily focused on container-grown seedlings as they are produced throughout Canada. People interested in a detailed discussion on the development of bare-root seedlings in the nursery and stock-type characterization prior to field planting should read Duryea and Landis (1984).

Forest companies throughout the world have been working towards effective silvicultural practices that are required to ensure maximum survival and growth of spruce seedlings on reforestation sites. This includes the use of site preparation and stand tending (i.e., fertilization and vegetation management) practices. In Canada, since 1991, the application of site preparation and stand tending silvicultural practices have been used on from ~700 000 to ~800 000 ha annually (Anonymous 1998). This indicates that there is a major commitment by the forest industry to ensure the successful development of young forest plantations. Examples that are discussed contain work that has been conducted with both bare-root and container-grown seedlings. The following discussion focuses primarily, although not exclusively, on silvicultural practices that are used throughout Canada. This treatise examines how northern latitude spruce species respond to intensive silviculture practices that are required to ensure plantation success.

Developing an understanding of the ecophysiological performance of northern spruce species is required to provide foresters with the knowledge of how spruce seedlings grow. From an anthropocentric perspective, this understanding can provide foresters with a spruce seedling's view of the effect of regeneration silvicultural practices on seedling performance. Thus, foresters would understand the ways in which silvicultural practices directly affect spruce seedling physiological response to specific environmental conditions (Colombo and Parker 1999). Physiological responses of spruce seedlings are reflected in their actual growth performance on reforestation sites. If silviculturists have a good understanding of spruce seedling ecophysiological performance, they can improve their ability to grow spruce seedlings within forest regeneration programs.

If one does not understand the underlying physiological processes, attempts to improve particular silvicultural practices, apply these practices to other environments, or to select improved genotypes are prone to failure (Margolis and Brand 1990). Understanding the ecophysiological performance potential of northern spruce species is a prerequisite for successful implementation of high-yield plantation forestry as defined by Gladstone and Ledig (1990).

Plant physiology deals with the functions and properties of plants, while ecology, as it relates to plants, is concerned with the mutual relationships of plants to other organisms and the environment. Thus, ecophysiology examines the physiological and morphological processes of plants in response to the surrounding environment. The primary focus of this treatise is on the physiological processes of northern spruce species at the whole plant level in response to the surrounding environment. This is because the effects of forestry practices are first recognized in the field at the whole plant level. Although the ultimate explanation for plant changes are often found at the cellular or subcellular level, the remedies are usually found at the whole plant level in terms of silvicultural treatments (Kramer 1986). Thus, foresters need to have an understanding of whole plant physiology to ensure a successful silvicultural program. Northern spruce species whole plant physiological processes to be discussed are water relations, gas exchange, mineral nutrition, freezing tolerance, and dormancy. The morphological development of northern spruce species in relation to environmental conditions is also discussed. This treatise also briefly examines major components of the seedling environment on both open reforestation sites and reforestation sites that retain a partial forest canopy and how these components influence seedling responses to site conditions.

Seedling establishment and subsequent growth on a reforestation site is paramount to successful forest regeneration. This success can only occur if foresters make their management decisions based on site-specific knowledge. This site-specific knowledge means understanding the ecological dynamics of a site and tailoring appropriate management strategies based on information about local environmental conditions, site history, disturbance regimes, community dynamics, and species habitat requirements (Kohm and Franklin 1997*b*). Spruce seedling performance depends on both inherent seedling growth potential and the degree to which environmental conditions allow this growth potential to be expressed. The inherent growth potential of spruce seedlings is related to morphological and physiological characteristics. Therefore, it is the response of spruce seedlings to site environmental conditions that ultimately determines seedling performance. It is recognized that how spruce species respond within the overall forest ecosystem is an important aspect in the management of northern forests. It is beyond the scope of this treatise to discuss aspects of silvicultural practices as they relate to the overall dynamics of the forest ecosystem and the management of these forests. In an attempt to synthesize this extensive body of information, a number of excellent publications have been written that summarize the state of knowledge on the ecology and management of North American forests in general (e.g., Barrett 1980; Larsen 1980; Waring and Schlesinger 1985; Kimmins 1987; Perry 1994; Kohm and Franklin 1997*a*; Walker 1998; Waring and Running 1998) and specifically on spruce species used in plantation forestry programs throughout North America (e.g., black: Larsen 1982, Van Cleve et al. 1986, Crook and Cameron 1995; Engelmann: Alexander 1987, Alexander and Shepperd 1990; interior: Dobbs 1972, Coates et al. 1994; Sitka: Peterson 1997; and white: Stiell 1976, Van Cleve et al. 1986). It is the intent of this treatise to have foresters develop an understanding of the ecophysiological processes of spruce seedlings and the influence of site conditions and silvicultural practices related to early plantation establishment. This appreciation of the ecophysiological processes of spruce species enables foresters to put site-specific management decisions within proper context of the northern latitude forest ecosystem.

This treatise is intended to synthesize the state of knowledge on the ecophysiological performance of northern spruce species. In an attempt to provide a complete understanding on the ecophysiological performance of northern spruce species, relevant information has been drawn from spruce species that are of primary interest in worldwide silviculture programs of the northern latitude forests. Thus, information is drawn from work on white, Engelmann, interior, black, red, Norway, and Sitka spruce species. In a few instances, supporting information is also included on work with Colorado (or blue) spruce (*Picea pungens* Engelm.). It is recognized that there is genetic variation in ecophysiological performance between, as well as within, northern spruce species. With this caveat in place, only general physiological response patterns of these spruce species are used to support the discussion. Ecophysiological performance of northern spruce species as it relates to genetic variation is recognized, and a discussion on this variation is the focal point of Section 4.

The treatise is designed so that the reader develops an initial understanding of spruce seedling's primary physiological processes and the importance of these processes when making silvicultural decisions. This treatise does not discuss all aspects of ecophysiological principles in complete detail. Further information on ecophysiological processes of plants can be found in a number of publications (Tranquillini 1979; Etherington 1982; Landsberg 1986; Kozlowski et al. 1991; Larcher 1995; Smith and Hinckley 1995*a*, 1995*b*; Kozlowski and Pallardy 1997; Lambers et al. 1998) and reviews specifically related to forest regeneration (Duryea and Brown 1984; Burdett 1990; Lavender 1990; Margolis and Brand 1990; Hobbs 1992; Lamhamedi and Bernier 1994).

This treatise has been written as a multilevel text which allows the reader to examine spruce ecophysiology at many different levels, depending upon their interest. Section 1 describes parameters of the "operational environment" defined by Spomer (1973). This approach allows the reader to develop an appreciation of biotic and abiotic factors that directly affect the spruce seedling environment. In the following sections the reader can examine spruce ecophysiology information from a number of different levels. Section 2 discusses basic physiological concepts as they relate to spruce species. Section 3 examines specific physiological response patterns of spruce species to important environmental conditions. Section 4 provides a series of examples of how genetic variation can affect the ecophysiological response of spruce species. Section 5 discusses the ecophysiological response of spruce species to silvicultural practices within the forest regeneration process. All related subsections are tied together by section reference links. This allows the reader to delve into a specific physiological process or silvicultural practice at any level of detail that is required for their intended purpose. In this way, this treatise can be used as a reference text to address specific topic areas that are related to the ecophysiological processes of northern latitude spruce species.

The treatise attempts to be comprehensive, though not exhaustive, in covering all aspects of the ecophysiological performance of northern latitude spruce species and the influence of currently used forest regeneration practices that are applied when seedlings are planted on reforestation sites. It is intended to provide foresters with enough information on these processes to enable them to understand what type of effects their silvicultural decisions are having on subsequent seedling performance. An understanding of these ecophysiological processes can enable foresters to make knowledgeable silvicultural decisions as they implement their forest regeneration programs, thereby improving spruce seedling survival and growth.

1 Reforestation site environmental conditions

Forest structure has a direct bearing upon the energy, hydrologic, and nutrient cycles that make up the environment of a forest ecosystem. This forest influence is described as the effect of a closed forest canopy on the environment of the land it occupies (Keenan and Kimmins 1993). When a forested stand is harvested through clear-cutting or the application of other silvicultural systems, the basic structure and function of the stand is altered. The alteration of the stand structure influences many aspects of the functioning of the future ecosystem. First and foremost, when a forest is harvested, total biomass (living and dead) is reduced. This reduction in total biomass results primarily from overstory removal, although the entire stand structure is altered. Stand structure refers to the vertical and horizontal arrangement of trees, shrubs, grasses, and forbes, as well as snags, downed logs, and the forest floor depth. As a result, primary ecosystem functions such as energy, hydrologic, and nutrient cycles are altered immediately and influence the flow of resources through the ecosystem (Fig. 1). It must be kept in mind that many aspects of the nonliving environment of a site are not greatly altered by a forest disturbance. Some of these site factors that are relatively unaffected by a forest harvesting activity are elevation, slope, soil depth, and texture (although there can be some alteration of soil structure), soil mineralogy, and regional climate (Keenan and Kimmins 1993). Forest disturbance has a direct effect upon the site microclimate, site water balance, and soil fertility, and these factors directly influence the physiological response of spruce seedlings after they are planted on a reforestation site.

The following general statements can be made about each of the primary ecosystem functions in relation to climax northern latitude forests and clear-cut forest regeneration sites (Fig. 1).

Energy cycle ⇒ Forest canopy removal results in a shifting of the energy balance. Radiant energy that was previously captured within the forest canopy is now intercepted at or near the soil surface. This change in energy distribution dramatically alters soil and air temperatures and evaporative demand near the ground where seedlings are planted.

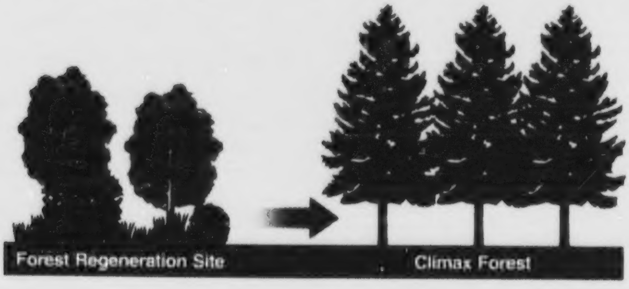
Hydrologic cycle ⇒ Inputs to the hydrologic cycle come primarily through precipitation and secondarily through downslope drainage. Losses occur through many sources, including interception of rainfall by vegetation, evaporation from plant and soil surfaces, soil drainage, and transpiration. Climax forested stands have high stand transpiration rates, resulting in a more regulated and reduced stream flow through the ecosystem. Conversely, forest regeneration sites are characterized by low stand transpiration, potentially readily available soil water, and increased stream flow out of the ecosystem. However, at the effective rooting depth of planted spruce seedlings, other vegetation cover competes for soil water, resulting in localized conditions of soil water deficit. Thus, reforestation sites present conditions in which seedlings are exposed to either low soil water at the effective rooting depth or excess soil water during the growing season.

Nutrient cycle ⇒ Nutrient cycling is slow in climax forests. Little nutrient mineralization occurs, with most nutrients bound in the biomass and organic matter on the forest floor of the site. On reforestation sites, however, the removal of biomass through harvesting reduces the overall nutrient content of the site. The remaining nutrient budget comes primarily from the forest floor organic matter, and is more rapidly cycled within the ecosystem through decomposition and mineralization.

The structure of a climax northern latitude forested stand is relatively stable, with little change occurring over extended periods of time (Fig. 1). Northern spruce encompasses species that are considered to be slow growing and long-lived, and have lower levels of overall physiological activity, making them well suited to the climax forest environment. Reforestation sites develop a secondary successional environment where early seral stage species start to occupy the site. Early seral stage species are fast growing and short-lived and have a high level of overall physiological activity. This causes rapid and dynamic changes in site canopy structure, and in patterns of water, energy, and nutrient use.

Fig. 1. Ecological structure of a reforestation site and a climax forest in temperate and boreal forest regions.

Energy	**Energy**
✦ Increased radiant energy to the soil	✦ Radiant energy primarily captured by the forest canopy
Water	**Water**
✦ Low stand transpiration ✦ High available soil moisture ✦ Increased streamflow	✦ High stand transpiration ✦ Reduced streamflow
Nutrients	**Nutrients**
✦ Increased decomposition ✦ Increased mineralization and nitrification	✦ Located in plant biomass, woody debris and organic matter ✦ Low mineralization and nitrification
Fast growing/short-lived species (High: transpiration, net photosynthesis, nutrient uptake)	***Slow growing/long-lived species*** (Low: transpiration, net photosynthesis, nutrient uptake)
Dynamic Stand Structure	**Stable Stand Structure**



Reforestation sites that have been created by the clear-cutting harvesting practice have environmental conditions that differ from the natural ecological conditions normally found by conifer seedlings (Spittlehouse and Stathers 1990; Keenan and Kimmins 1993). These sites have high competition dynamics, that is, the soil substrate is left relatively intact, which allows shrubs and forbs to rapidly reoccupy the site (Margolis and Brand 1990; Keenan and Kimmins 1993) (Section 5.5). The difference in the physiological activity and growth patterns between early seral stage species and spruce seedlings (i.e., a climax species) affects utilization of site resources. As a result, the dynamics that occur between the early seral stage species and spruce seedlings have large ramifications on the success of reforestation operations in developing forest plantations.

Reforestation sites can be created with the application of silvicultural systems that retain a partial forest canopy. These alternative silvicultural system approaches retain part of the forest structure, which enables the site to sustain more components of a mature forest stand. The use of partial forest canopy retention systems within northern latitude forests influence the microclimate at the location where seedlings are planted. Environmental changes that occur with the use of these partial forest canopy retention systems and their effects on spruce seedling performance are discussed later in this treatise (Section 5.6).

It is beyond the scope of this treatise to examine in detail how these ecosystem functions are altered after the practice of clear-cut harvesting and how ecosystem processes influence the performance of newly planted forest plantations. Readers interested in understanding how ecosystem functions are altered by a disturbance, and the subsequent development of a forested stand within an ecological successional context, should refer to Bormann and Likens (1981), Mooney and Godron (1983), Keenan and Kimmins (1993), and Perry and Amaranthus (1997) for excellent discussions on the subject.

Reforestation site microclimate broadly reflects the regional climate, but the microclimate around a seedling is influenced by the interaction of regional weather conditions (i.e., based on latitude and elevation), specific site factors, and silvicultural activities. Knowledge of atmospheric conditions, primarily the radiation energy and water that are exchanged between seedlings and the environment, is essential in understanding the influence of silvicultural practices on seedling survival and growth. Site factors such as topography, aspect, vegetation cover, and soil type can modify the effects of weather conditions. Soil nutrition and its effect on seedling development is dependent upon the interaction between soil type and the reforestation site microclimate. The concept of an "operational environment" defined by Spomer (1973) is appropriate to the discussion of the seedling environment, as it includes only those biotic and abiotic factors directly interacting with or capable of being exchanged with the seedling.

This section briefly defines the main concepts of an operational seedling environment. The intent is to provide enough of an understanding of the operational environment so that one has an appreciation of how it can affect the ecophysiological processes of spruce seedlings that are growing on reforestation sites. For detailed information on plant microclimate and forest meteorology, readers are directed to a number of excellent sources (Geiger 1980; Gates 1980; Nobel 1991; Jones 1992).

1.1 Radiation

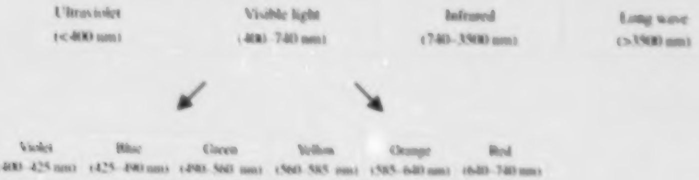
1.1.1 Radiation transmitted through the atmosphere

Solar radiation as a general term refers to energy transmitted to the earth by the sun. It is measured in wavelengths, with the length of the wave determining the property of the particular ray. Exchange of solar radiation in the biosphere takes place within an approximate wavelength range of 300–100 000 nm. Solar radiation in this spectral range is generally described in Fig. 1.1.1*a*.

Solar radiation that is visible to the human eye is called visible light. This portion of the solar spectrum also directly affects the ecophysiological processes of plants. This area of the solar spectrum has wavelengths measuring from 400 to 740 nm (Fig. 1.1.1*a*). Light comprises 40–50% total incident solar radiation, and is very important, as it has a major impact on the biological processes of plants (Nobel 1991; Salisbury and Ross 1992). This light region of the solar spectrum can be broken down into three regions. First, the violet and blue region of the solar spectrum (400–490 nm) is involved in photosynthetic activity (Sections 2.2.3 and 3.1) and nonphytochrome photomorphogenesis (Section 2.5). Second, the green, yellow, and orange region of the solar spectrum (490–640 nm) is an area of low photosynthetic effectiveness. Third, the red region of the solar spectrum (640–740 nm) is involved in photosynthetic activity and phytochrome photomorphogenesis (Section 2.5). These three regions of the spectral range of visible light have a direct bearing on the performance of spruce seedlings.

Solar radiation in other regions of the overall solar spectrum relevant to ecophysiological processes of plants is found just above and below the visible, or light, region of the solar spectrum (Fig. 1.1.1*a*). Radiation from shorter wavelengths (wavelengths from 300 to 400 nm), such as ultraviolet rays, are very high in energy and can damage and cause mutations in the genetic material of living cells. Far-red light includes wavelengths just longer than red light (740–800 nm) and influences the plant phytochrome system which controls the photomorphogenesis response of plants (Section 2.5). Approximately one half of the solar energy is shortwave infrared radiation which consists of wavelengths in the 800–3500 nm range that act to warm the environment. Solar energy beyond 3500 nm

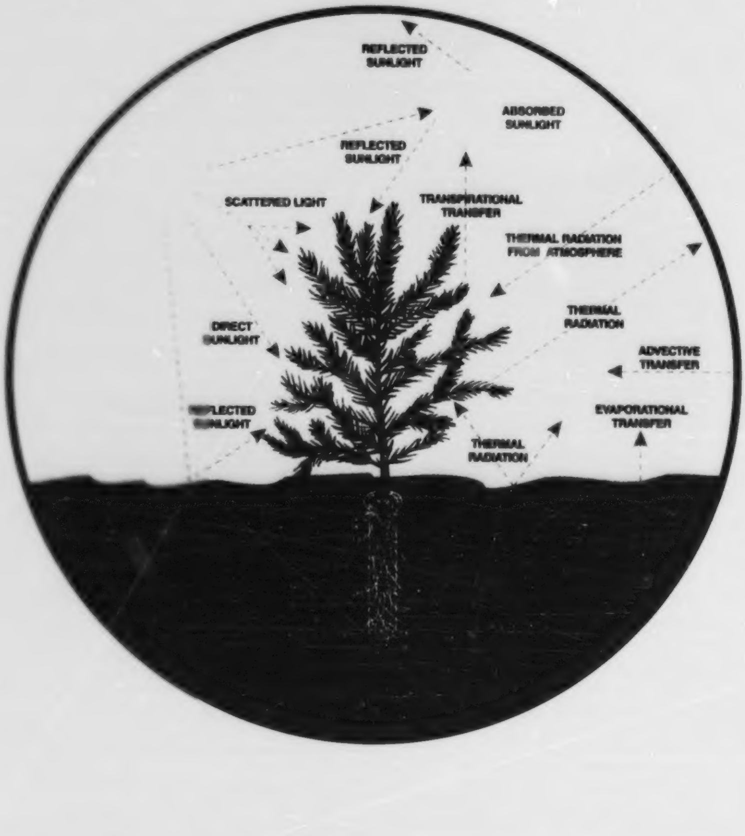
Fig. 1.1.1*a*. The spectrum of radiant energy.



is called long-wave or thermal radiation. The intensity of thermal radiation is a function of the temperature of the object emitting this form of radiation. This energy is emitted by plants, animals, downed woody plant material, and the sky, and is an important component of the energy balance (Fig. 1.1.1*b*) (Section 1.2), thus influencing seedling physiological processes related to temperature (Sections 3.3 and 3.5.1). For purposes of this discussion, solar radiation refers to all regions of the solar spectrum (i.e., ultraviolet rays, visible rays (light), and shortwave infrared rays), while photosynthetically active radiation (PAR) refers to the light region, and thermal radiation refers to longer wavelengths of the solar spectrum (Etherington 1982).

The solar radiation received by a particular object or site can be quantified as the flux density. The solar constant (1360 W m^{-2}) is the flux density on a plane perpendicular to the sun's rays at the top of the atmosphere. Flux density at the surface of the earth depends upon the location, time of day and the time of year because of changes in (*i*) path length of the solar beam, (*ii*) spectral characteristics of objects encountered in this path, and (*iii*) orientation of the surface of the object relative to the solar beam. Photosynthetically active radiation received at

Fig. 1.1.1*b*. Representation of energy exchange between a spruce seedling and the environment.

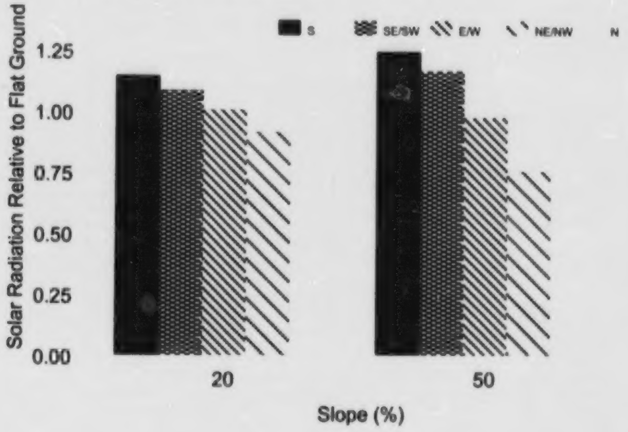

REFLECTED SUNLIGHT
ABSORBED SUNLIGHT
REFLECTED SUNLIGHT
SCATTERED LIGHT
TRANSPIRATIONAL TRANSFER
THERMAL RADIATION FROM ATMOSPHERE
THERMAL RADIATION
DIRECT SUNLIGHT
ADVECTIVE TRANSFER
REFLECTED SUNLIGHT
EVAPORATIONAL TRANSFER
THERMAL RADIATION

sea level under full sunlight conditions is 450 W m^{-2} or 2000 μmol m^{-2} s^{-1}. Thus, seedlings receive solar energy as direct light from the sun, or as light that has been modified as it passes through the atmosphere or is reflected off objects.

Solar radiation that has been modified along its path is referred to as scattered or diffuse, as opposed to direct, shortwave radiation. When solar radiation is scattered, absorbed, and reflected by substances in the atmosphere, such as gases, water droplets, dust, and pollutants, the quantity of light is decreased, and the spectral properties are altered (Fig. 1.1.1*b*) (reviewed by Etherington 1982; Kimmins 1987; Kozlowski et al. 1991). This results in a more even wavelength distribution and an overall reduction in flux density. As incoming solar radiation passes through the atmosphere throughout the year, ~25% is absorbed by ozone, water dust, and clouds. Another ~28% is reflected by clouds, scattered dust, soil, vegetation, and water. The remaining ~47% reaches the reforestation site as either direct (~22%), scattered (~10%), or reflected (~15%) radiation. The scattering of light can increase the amount of light reaching the site (i.e., a 5–10% increase) when the sky is not completely clear and on days with broken cloud cover. It is interesting to note that snow cover has the highest albedo, other than cloud cover, for diffuse reflection for the total range of solar radiation (Geiger 1980). This is worth noting because northern latitude regions can have snow cover for up to 8 months of the year (Section 1.2.1). Thus, the amount of solar radiation reaching an open reforestation site changes throughout the year, depending upon the presence of snow cover which causes an increase in the amount of solar radiation reflected away from the site. The actual amount of solar radiation reaching a reforestation site on any given day is dependent upon time of the year, weather conditions, and particulates in the atmosphere.

Topographic effects on irradiance are exhibited on both a stand and microsite scale, and have important implications for regeneration efforts. Solar irradiance

Fig. 1.1.1c. Annual amount of solar radiation received on selected aspects and slopes at 50° N lat. relative to the solar radiation received on flat ground (i.e., flat ground = 1.0) (adapted from Stathers and Spittlehouse 1990).



deviates from the perpendicular diurnally with changes in solar elevation and angle, and seasonally with the azimuth angle of the sun. Slope and aspect have significant effects on the radiation load of a site or microsite by affecting the angle in which solar radiation is received (Maguire 1955; Geiger 1980; Spittlehouse and Stathers 1990). For example, on a northern latitude site, the annual amount of solar radiation received by a site varies, depending upon whether it has a north- or south-facing slope and the slope angle (Fig. 1.1.1*c*). Thus, steeper south-facing slopes located in the northern latitudes receive greater radiation loads throughout the year.

1.1.2 Radiation transmitted through the forest canopy

Solar radiation entering a conifer forest is modified as it is absorbed, reflected, or passed through the forest canopy before it reaches the forest floor. The following discussion examines how the canopy of northern latitude forests alters light received at the top of the forest canopy as well as the quantity and quality of light reaching the forest floor.

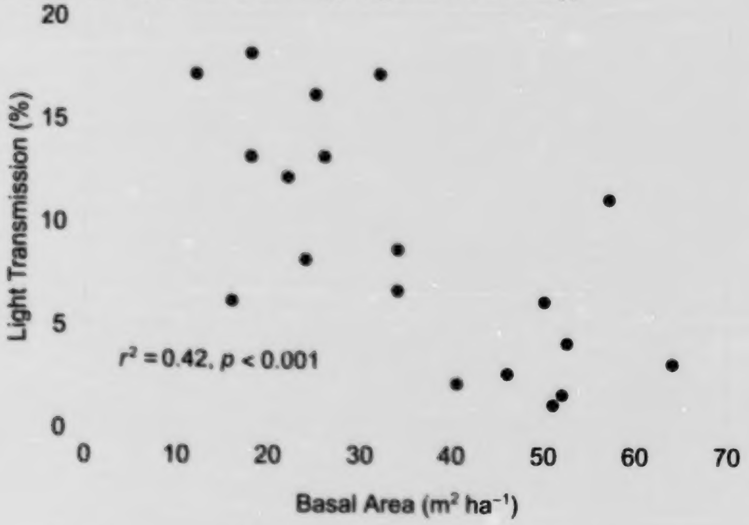
Radiation reaching the upper canopy of a northern latitude forest is partially reflected by the leaves and branches of the trees within the canopy. Larcher (1995) estimates that ~10% of solar radiation entering a conifer stand is reflected back into the atmosphere, while the amount of radiation reflected from a spruce forest canopy can range from 4 to 14%. The variation in reflectivity is due to the glaucous character of spruce needles (i.e., needles covered with fibrillar wax), and the height and density variations of the stands (Jarvis et al. 1976). Thus, stand density and species composition can affect the amount of reflected solar radiation.

The structure and species composition of the canopy, stand density, the variation in the position of the sun, sky conditions, and the proportion of direct to diffuse solar irradiance determines the amount of radiation received by understory vegetation (Federer and Tanner 1966; Reifsnyder et al. 1971; Jarvis et al. 1976). The forest vegetation type determines the leaf area and crown density of the canopy at various levels within the forest vegetation structure (Vezina and Pech 1964; Reifsnyder et al. 1971; Hungerford 1979), although twigs and branches within the forest canopy also contribute to the extinction of light down through the canopy (Jarvis et al. 1976).

The amount of radiation absorbed by vegetation declines as it travels down the canopy structure of a northern latitude conifer forest: 79% is absorbed by the upper canopy, 9% by the secondary canopy, and 2% reaches the forest floor (Larcher 1995). In forests dominated by conifers, the amount of stand basal area has a direct impact on light quantity received at the forest floor throughout all seasons (Fig. 1.1.2*a*). Seasonal differences in light canopy transmission of 5–10% can occur in boreal conifer forests due to the timing of needle flush (Chen 1996).

In forests where the canopy is primarily made up of deciduous species, light transmission through the canopy is higher during the spring, before leaves have

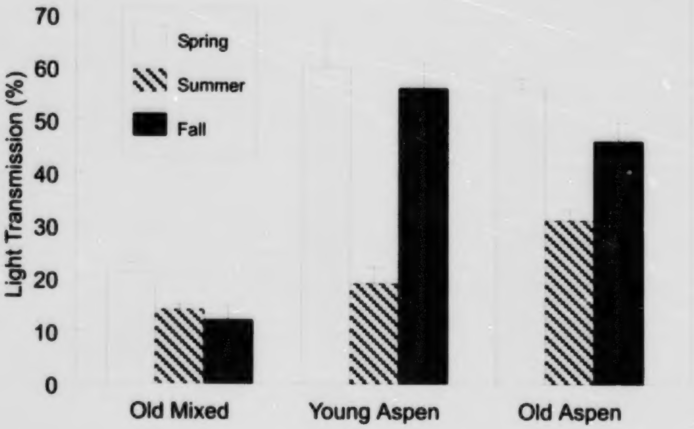
Fig. 1.1.2*a*. Relationship between average light transmission and the stand basal area for conifer-dominated stands. Data presented represents a summary of observations from various temperate and boreal forests (compiled by Messier 1996). Transmission was calculated as light below the canopy / light above the canopy.



developed, and in the fall, after leaves have dropped. For example, in boreal forests dominated by aspen (*Populus tremuloides* Michx.), the amount of light that reached the forest floor in relation to light level above the forest canopy was very high during the spring and fall, but dropped to a low level during the summer, compared to consistently low light reaching the forest floor in an old mixed (i.e., spruce–aspen) forest (Fig. 1.1.2*b*). In other studies, a deciduous overstory reduced total solar radiation, reaching 1.2 m above the forest floor, to <20% of total solar radiation recorded above the forest canopy during the summer, after leaves have developed (Groot et al. 1997; Messier et al. 1998). All of these studies found that there was a dynamic seasonal pattern in the range of light transmission through a deciduous forest canopy.

Sun flecks occur throughout the understory of a forest as solar radiation beams pass directly through a "hole" in the canopy (Etherington 1982). These sun flecks provide most of the energy for photosynthesis of understory plants (Reifsnyder et al. 1971; Chazdon and Pearcy 1991). The composition of the overstory canopy affects the distribution and duration of sun flecks, thereby creating a variable light environment on the forest floor. Hardwood forests have a lower proportion of sun flecks at higher light levels (i.e., up to 500 $\mu mol\ m^{-2}\ s^{-1}$) compared to conifer canopies (Messier et al. 1998). Messier and associates (1998) attributed this to an even distribution of leaves in the hardwood canopy compared to a conifer canopy that can have dense crowns with well-defined holes between adjacent trees. Direct measurements of the light environment under a variety of forest canopies on a clear, sunny day indicate that sun flecks can provide from 20 to 80% of the light received by understory plants (Pearcy

Fig. 1.1.2*b*. Seasonal pattern of average light transmission (mean + SE) through boreal forest canopies in west-central Alberta (54° N lat.) (adapted from Constabel and Lieffers 1996). Transmission was calculated as light below the canopy / light above the canopy.



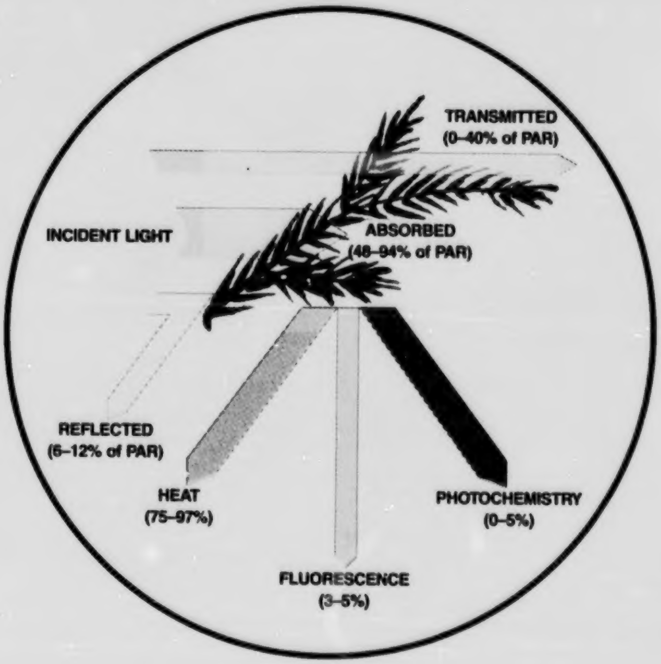
1990). Thus, spruce seedling photosynthetic performance on reforestation sites is determined by the nature of the vegetative canopy that develops from growth of competing vegetation on clear-cut reforestation sites, or by the choice of silvicultural systems with a specific residual forest canopy density and species composition.

Light of altered spectral quality occurs in two main terrestrial situations: under leaf canopies, and at high elevations where ultraviolet light is enhanced (Fitter and Hay 1983; Vezina and Boulter 1966). The red to far-red light ratio remains relatively constant at 1:10 above the forest canopy (Holmes and Smith 1977). As sunlight passes through the canopy, red (640–740 nm) and blue (425–490 nm) wavelengths are depleted because of absorption and scattering of light, thereby turning the spectral distribution of light under a forest canopy towards the yellow to green portions of the spectrum (Gates 1980; Kendrick and Frankland 1983). This change in the spectral distribution of light can reduce the photosynthetic capacity of understory species. Near infrared light (740–800 nm) also becomes enriched as light passes through the canopy due to the high reflectivity and low absorptivity of these wavelengths by foliage within the canopy (Jarvis et al. 1976). Thus, vegetation canopies can reduce the red to far-red light ratio (Federer and Tanner 1966; Smith and Morgan 1982). As a result, a light ratio in the range of 1:10–1:75 is common below spruce forest canopies (Smith 1994). This alteration of the red to far-red light ratio can influence the phytochrome system (Section 2.5) and morphological structure (Sections 3.1 and 2.6.1.3) of spruce seedlings.

1.1.3 Radiation at the needle surface

The amount of light absorbed by spruce needles is dependent upon epidermal and hypodermal layers (Section 2.2.3), anatomical (sun or shade needles) characteristics (Section 2.6.1.3), and pigment composition (chlorophyll and accessory pigments) (Section 2.6.1.3). Light that reaches the spruce needle surface is either absorbed by the needle (48–94%), reflected (6–12%), or transmitted (0–40%) (Fig. 1.1.3). Of the light absorbed by the spruce needle, approximately 75–97% is lost as heat (i.e., transpiration, sensible heat, and thermal radiation, Fig. 1.1.1*b*) and 3–5% goes into fluorescence emission. Only up to 5% of the light absorbed by plant chlorophyll is actually used in the light-activated processes of photosynthesis (Nobel 1991). Thus, only a very small fraction of the solar radiation transmitted to the earth by the sun actually goes into the process of photosynthesis in plants.

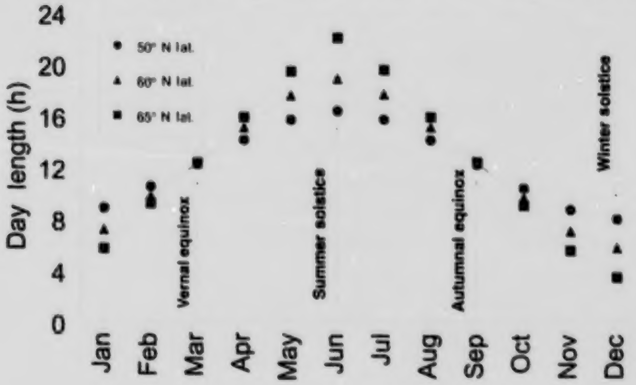
Fig. 1.1.3. The disposition of light (photosynthetically active radiation, PAR) reaching the needle surface of an spruce seedling (adapted from Larcher 1995; Nobel 1991).



1.1.4 Seasonal variation in day length

The length of day and night, and thus the amount of radiation received in the northern latitude forest, is dictated by the annual revolution of the earth around the sun. Seasonal changes in day length are due to the fact that the earth is tilted at an angle of 23.5° from perpendicular and that the earth has a 1-year elliptical orbit around the sun. Day length is defined as the interval between sunrise and sunset (i.e., when the upper edge of the disc of the sun appears to be exactly on the horizon). Northern latitude forests of the world span from approximately 50 to 70° N lat. Due to the higher latitudes of these forests and the seasonal change in the earth–sun relationship, there is a wide range in seasonal variation of day length and thus in the amount of radiation reaching the forest (Fig. 1.1.4). Within northern latitude forests, the daylight period is 12 h long at the vernal and autumnal equinoxes. At 50 and 65° N lat., the daylight period changes from 8 and 3.5 h in length, respectively, on the day of the winter solstice, to 16.3 and 22 h in length, respectively, at the summer solstice. At 66°30′ N lat., the daylight period reaches 24 h on the summer solstice and 0 h on the day of the winter solstice. Thus, any forest locations north of this latitude has extended periods of continuous daylight around the summer solstice and periods of continuous darkness around the day of the winter solstice. Seasonal changes in daylight, in turn, have a major influence on seasonal temperature patterns within the northern latitude forest (Section 1.2.1). These seasonal changes in day length and radiation (i.e., temperature) have major effects on the seasonal phenological cycle and the physiological response of spruce species to field site environmental conditions (Sections 2.5 and 3.9).

Fig. 1.1.4. Cycle of day length (i.e., the interval between sunrise and sunset), on the 21st of each month, at a range of latitudes that span the northern latitude forest.



1.2 Energy balance

The radiant energy balance of an object (e.g., a seedling), describes the balance between incoming sources (e.g., solar irradiance) and outgoing sources (i.e., long-wave emittance) of energy. This is because the energy balance of an object is a result of the second law of thermodynamics which states that heat passes spontaneously only from a system of higher temperature to a system of lower temperature. An object receives solar radiation (direct and diffuse) and long-wave radiation from the sky and surrounding objects (a function of temperature) (Fig. 1.1.1*b*). An object loses radiation by reflection of the incident solar radiation, or emission and reflection of long-wave radiation (based on an object's temperature). All objects above the temperature of absolute zero emit energy by radiation and, in turn, absorb radiant energy. This process is described by Stefan–Boltzmann's equation which states that the amount of energy radiated by an object is a function of the fourth power of the absolute temperature of its surface. Real objects are not perfect radiators and have emissivities less than unity (i.e., <1). For example, the long-wave emissivity of a leaf is >0.95–1.0, a conifer forest canopy is >0.90–1.0, wet soil is between 0.90 and 0.95, and new snow is 0.82. Thus, all objects transfer heat with the emission rate dependent upon the temperature and emissivity of the object.

On a reforestation site, the energy balance of a seedling is a function of the relative surface temperature and the absorbance and emittance characteristics of all parts of the ecosystem. The disposition of energy from all sources is described by developing an energy budget for a seedling. This budget depicts the complexity and consequences of energy exchange by a seedling. The energy balance of a seedling can be expressed as follows:

$$R_\mathrm{n} = H + \mathrm{LE} + S + M$$

where net radiation (R_n) is the balance between incoming and outgoing longwave and shortwave radiation. The R_n can be dissipated as sensible heat flow (H), as latent heat flux (LE, transpiration and (or) evaporation), and as a change in heat storage (S) (a temperature change) of the object. The change in S reflects a net increase or decrease in accumulated energy. Metabolic energy (M) of the seedling (i.e., photosynthesis or respiration) is sometimes considered in the energy balance of plants, although it is usually not important because its share in the overall energy budget is very small, on the order of 1–2%. The significance of the energy balance is how it affects the temperature of a seedling. Since only a small portion of energy from incoming solar radiation is converted into M during the day, the rest of the energy is transferred to the surrounding ecosystem, as H or LE, or it is retained as S. In reality, a substantial portion of solar energy absorbed by a plant is transferred back to the surrounding ecosystem through conduction or convection, or is used in LE transfer through transpiration of water by leaves.

Sensible heat is the movement of energy between an object and the air. This occurs in the form of conduction or convection. Conduction is the transfer of energy through molecular action. This occurs primarily between solid objects and is very important in describing the thermal properties of soils (Section 1.2.4). Convection is the transfer of energy due to mass movement of the air. This energy transfer process occurs through either horizontal air movement (i.e., forced convection) or a transfer by upward or downward moving air (i.e., free convection). Convective energy transfer from a seedling is proportional to the temperature difference between leaves and air and inversely proportional to thermal resistance and boundary layer thickness. A discussion of boundary layer around spruce needles is presented in this treatise (Section 2.1.2), and there is a discussion of how needle temperature can be altered by shoot morphology (Section 2.6.1.3).

Latent heat is the change in the state of water between vapor, liquid, and solid forms, which is accompanied by liberation or consumption of energy. This occurs when water is lost through the process of transpirational transfer from the vegetation and evaporational transfer from the plant surface or soil. Energy required to overcome the intermolecular attraction of water molecules and change water from a liquid to a gaseous state requires 43 kJ mol^{-1} water (at 25°C). The loss of this latent heat through vaporization has a significant cooling effect and is a mechanism of leaf temperature regulation. An equal amount of energy is liberated with the condensation of water vapor. In addition, approximately 5 kJ mol^{-1} water is released or absorbed during the freezing of water or the melting of ice. Formation of dew and frost are processes by which latent heat is gained by plant surfaces. These factors that alter the latent heat flux, thus temperature within the seedling environment, also alter the hydrologic balance of the site and the transpirational process of the seedling (Fig. 1.3).

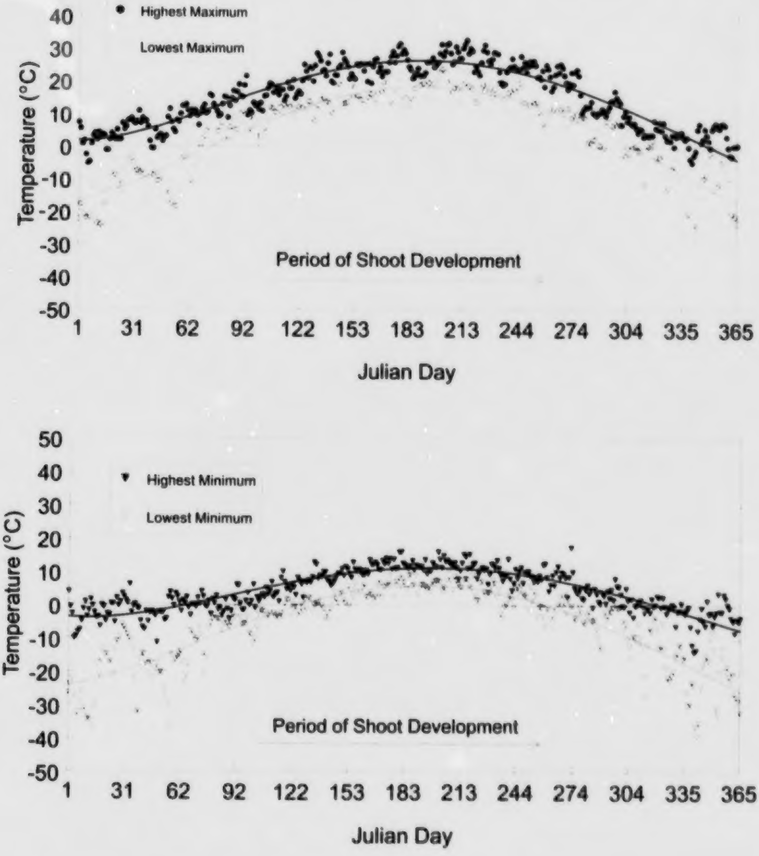
A spruce seedling planted on a reforestation site, the surrounding vegetation complex, and the soil absorb the downward flux of shortwave radiation from the sun and long-wave radiation from the atmosphere. They exchange energy amongst themselves and emit energy to the atmosphere as long-wave radiation. The difference between this absorption, temporary storage, and reradiation of energy throughout the season, or on any individual day, is a measure of the energy available to drive the environmental processes of the site. Components of the plant's energy balance are positive or negative, depending upon whether there is a gain or loss of energy with the surrounding environment. The relative amount of energy flux from each component depends upon the partitioning of R_n, which is influenced by the humidity, temperature, and wind speed (i.e., advective transfer) of the air, the soil water content, and soil thermal properties. The following sections briefly describe how these environmental variables are affected by the energy balance around the seedling. Readers are referred to Jones (1992) for a more detailed discussion of the radiation balance at the earth's surface.

1.2.1 Seasonal temperature fluctuations

Latitude influences seasonal day length (Section 1.1.4) which in turn alters the length of time the site warms and cools during each day. General temperature patterns throughout the northern latitude forests are dominated by large seasonal air masses that determine regional air temperatures. Northern latitude forest locations (i.e., above 50° N lat. in North America, Europe, and Asia, and in more southerly mountain ranges) have mean summer temperatures that range from approximately 10 to 20°C and mean winter temperatures that range from 0°C in more coastal and southern locations to –40°C in more continental and northern locations (Miller 1971). The occurrence of low temperatures and frost are quite high throughout northern latitude forests; more coastal and southern locations having average annual minimum temperatures between –10 and –40°C, and more continental and northern locations having average annual minimum temperatures below −40°C (Larcher and Bauer 1981).

An example of seasonal air temperature patterns for a specific site within the northern latitude region shows that maximum air temperatures can range from 0°C to as high as 25°C throughout the year (Fig. 1.2.1*a*). Maximum air temperatures can be above 10°C from late February through October. Minimum low air temperatures can range from −25°C to as high as 5°C throughout the year, and at any time during the year, air temperatures can dip below 10°C. During the winter months (December through February), minimum air temperatures are regularly below −20°C and can occasionally be as low as −40°C.

Fig. 1.2.1*a*. Average seasonal air temperatures (maximum and minimum taken at 1.3 m) throughout the entire year for this northern latitude location (Prince George, B.C., 54° N lat.) from 1992 to 1995 (adapted from data provided by R. Scagel). (Further information on the period of active shoot development for spruce can be found in Section 2.6.1.)



Soil temperatures in northern latitude locations are also dominated by the same large seasonal air masses that determine the regional air temperatures. These seasonal air masses subsequently influence seasonal snow-cover patterns, which in turn influence soil temperature patterns. Throughout the year, continental locations within the northern latitude forests can have snow cover from 6 to 8 months every year (Mellor 1964). Within these continental locations, permafrost normally extends down to 65–60° N lat., with patchy permafrost found as far south as 50° N lat. (Ives 1974). More southerly continental locations typically can have as little as 2–4 months of snow cover each year (Mellor 1964). Throughout Europe, the United Kingdom, and coastal locations in North America and southern Scandinavia, snow cover occurs every year for up to 2 months, but the snow pack is unstable (Mellor 1964). The presence of snow cover tends to keep near-surface soil temperatures just below 0°C, because the snow pack acts as an insulating layer that reduces the rate of heat transfer from the soil to the colder air (Geiger 1980). Thus, near-surface soil temperatures in northern latitude forests do not start to increase much above 0°C until after the snow pack melts during the spring. Growing season soil temperatures are highly variable across the landscape because of the effects of latitude, slope, and aspect on the daily and seasonal duration of solar radiation reaching the soil surface (Section 1.1.1). In addition, soil temperature variability between sites is also influenced by site drainage, vegetation, and snow cover which alter the soil thermal regime. Thus, it is hard to provide a generalized growing season soil temperature pattern that is applicable to all northern latitude forest locations.

An example of seasonal soil temperature patterns for a specific site within the northern latitude region shows that soil temperatures increased above 0°C after the snow pack melted in April and then increased to 7.5°C during May when reforestation planting programs are usually initiated (Fig. 1.2.1*b*). Soil temperatures increased during the middle of the growing season to around 16°C, but then started to decline during the latter part of the summer. Soil temperatures (at 10 cm) can remain below 12°C throughout most of the growing season on reforestation sites located at higher elevations within the northern latitude forest (Sections 5.5.2 and 5.6). Soil temperatures continued to decline during the fall until the site was covered with snow, and then soil temperatures remained at 0°C throughout the winter.

Geographic factors within a specific region influence the local site energy balance which determines temperatures on a specific northern latitude reforestation site. Elevation of the site determines how rapidly site temperatures decline because radiative cooling is greater at higher elevations at the same latitude. In mountainous regions, the mean and absolute minimum temperatures drop by an average of 0.45–0.65°C per 100 m of elevation gain (Sakai and Larcher 1987). Slope and aspect also influence the amount of solar energy that is received on a reforestation site, with south-facing aspects receiving more solar energy (Fig. 1.1.1*c*). Thus, south-facing slopes have warmer temperatures throughout

Fig. 1.2.1*b*. Average soil temperature (at 10 cm) throughout the year for a northern latitude location (Prince George, B.C., 54° N lat.) (adapted from Stathers and Spittlehouse 1990).

the year than north-facing slopes (Spittlehouse and Stathers 1990). Each reforestation site within northern latitude forests has its own specific seasonal and daily range of temperatures based upon the site's geographic location.

The forest canopy reduces daytime solar radiation and long-wave radiative cooling at the soil surface by retaining a majority of the radiative transfer within the canopy. Removal of the canopy shifts the focal point of the energy balance to the atmosphere near the soil surface, and can result in the soil surface receiving 10–20 times more shortwave radiation on a clear, summer day (Fowler and Anderson 1987; Spittlehouse and Stathers 1990). As a result, daytime air temperatures at seedling height on a clear-cut site are greater than those found in a forested stand (Fig. 1.2.1*c*). Removal of the forest canopy also increases nighttime long-wave radiative cooling from the atmosphere near the soil surface. This can cause nighttime air temperatures at seedling height on a clear-cut site to be lower than those found in a forested stand (Fig. 1.2.1*c*). Solar and thermal radiation provide energy to warm the soil (Fig. 1.1.1*b*). Removal of the forest canopy allows solar radiation to reach the soil surface and cause an increase in seasonal temperature of the soil. For example, a mature white spruce stand has only 74% of the growing season soil heat sums, at 10 cm, that occur on a clear-cut site (Fig. 1.2.1*d*). These warmer soil temperatures on clear-cut sites can lengthen the growing season by increasing the number of days when root zone temperatures exceed the minimum temperature required for growth (Stathers and Spittlehouse 1990). This removal of the forest canopy can result in up to a 5°C increase in average soil temperatures throughout the growing season (Hungerford 1979; Childs et al. 1985) (Section 5.5.2). Removal of the forest canopy can create greater air temperature extremes for the atmosphere near the soil surface and increase the soil temperatures on any given day during the growing season.

Fig. 1.2.1*c*. Difference in air temperature (at 30 cm) throughout the growing season for a northern latitude location (central interior of British Columbia, 55° N lat.) in a mature aspen forest (aspen site is the reference and is equal to 0°C) compared to a clear-cut site (adapted from data provided by S.C. DeLong and R.M. Sagar). Growing season maximum, minimum, and average air temperatures under the aspen forest canopy were 19.2, 5.6, and 11.3°C, respectively. The approximate periods when leaf development (LDv) and leaf drop (LDr) occurred in the aspen canopy are designated by the arrows.

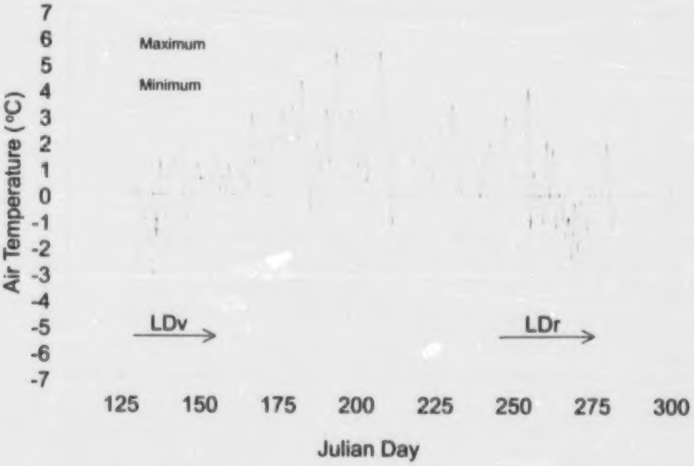
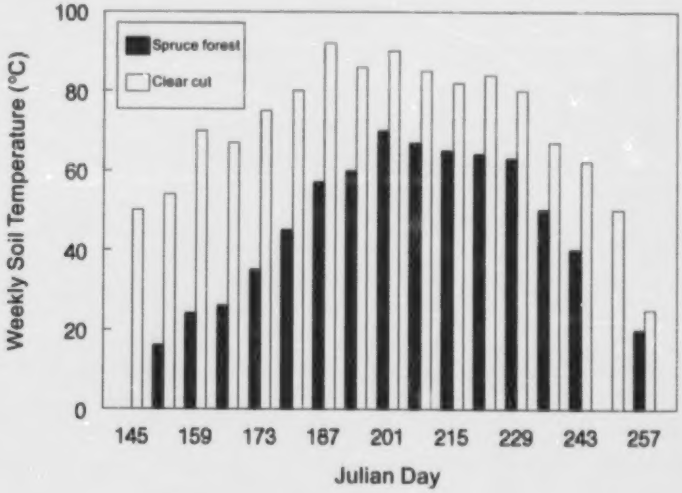


Fig. 1.2.1*d*. Weekly soil temperature sums (i.e., degree–day sums above the base temperature of 5°C), at 10 cm, throughout the growing season for a northern latitude location (Tanna River, Alaska, 64° N lat.) in a mature spruce forest and a clear-cut site (adapted from Viereck et al. 1993).

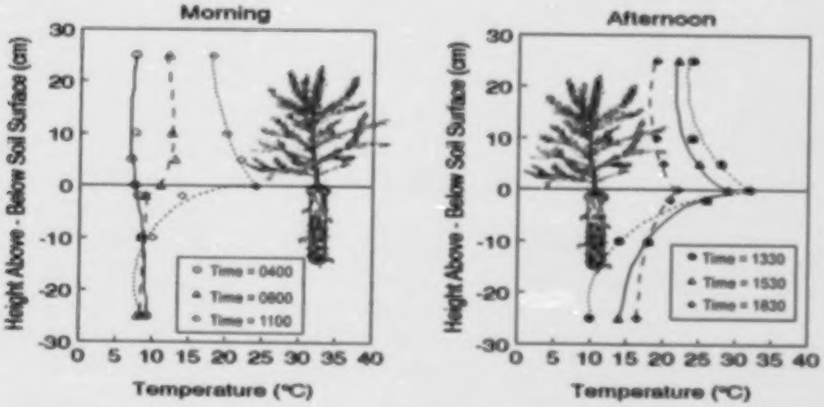


1.2.2 Daily temperature fluctuations

The energy balance of both the atmosphere near the soil surface and of the upper portions of the soil profile are of great importance to forest regeneration efforts because these are the regions that determine the daily seedling environment. The daily exchange of shortwave and thermal radiation, plus heat energy between the atmosphere and soil surface, affects the daily temperature microclimate around seedlings on an open reforestation site (Fig. 1.1.1*b*). Typically, under clear skies, the soil profile is slightly warmer than the atmosphere just before dawn (Fig. 1.2.2). In the summer, the soil has the highest yearly temperatures (Fig. 1.2.1*b*) and stored heat. Thus, at night, heat is lost from the ground to the sky as thermal radiation, with heat stored in the soil transferred to the soil surface. During the morning, net radiation is positive, as energy gained is greater than that lost, and the air, soil surface, and upper soil temperatures begin to increase (Fig. 1.2.2). This positive input of net radiation into the region near the soil surface continues until early afternoon, when air and soil surface temperatures have reached maximum daily values.

Maximum daily air temperature typically lags behind that of the peak period of incoming solar radiation such that peak air temperature occurs about 2 h after the time of maximum shortwave radiation flux density (at 1330 h, Fig. 1.2.2) (Maguire 1955). This time lag is the result of movement of heat (also called the soil heat flux) into the soil during morning hours. Soil acts as a sink for the temporary storage of solar energy at this time, and soil heat flux begins to warm the upper region of the soil. Comparatively, large radiation inputs are generally necessary to raise the soil temperature because of its high volumetric heat capacity (Section 1.2.4). Sensible heat loss from the ground, rocks, and plants warms the air during the day, with warming reaching a maximum by mid afternoon. The air

Fig. 1.2.2. Diurnal change in soil (at –2, –10, and –25 cm), soil surface, and air temperatures (at 5, 10, and 25 cm) around a conifer seedling planted in a light-colored mineral soil over a midsummer day on an open reforestation site (Grossnickle and Reid 1984*a*).



closest to the ground retains the most heat. Maximum daily air temperature at seedling height can be 10°C higher than air temperatures at 2 m, with soil or litter surfaces up to 30°C higher (Geiger 1980; Spittlehouse and Stathers 1990).

Due to the relatively slow transfer of heat through the soil, soil temperatures still continue to increase during the afternoon even as air temperatures start to decline (Fig. 1.2.2). As a result, air and upper soil temperatures are similar by the early evening hours. During the night, the gradient for heat exchange is reversed as air temperature declines. Heat is transferred to the night sky, with the soil acting as a source of heat for the atmosphere as the sensible heat flux is directed away from the surface. Soil temperature also decreases because the soil surface has a net loss of long-wave radiation to the atmosphere. These energy transfer processes demonstrate wavelike patterns of diurnal changes in the soil temperature profile, with a decreased amplitude at greater depths.

1.2.3 Growing season frost events

Removal of the canopy can also affect the seedling environment by increasing the potential for frosts during the growing season. Two types of frost events can occur on reforestation sites: inflow of a cold air mass and radiative frost. Both types of frosts are influenced by the reforestation site characteristics of elevation, slope position, slope angle, topography, and latitude.

Frosts occur when air (at temperatures below the freezing point) flows or is blown onto a site. This occurs on a regional scale when frontal activity (i.e., a cold air mass) moves onto a site, or on a local scale, with the downslope flow of freezing air through a valley, or by ponding in low-lying locations across the landscape. These frost events are directly influenced by slope position and angle. Slope position affects the size of a potential cold air source, while slope angle affects the rate of cold air drainage and the potential for air mixing (Geiger 1980). Topography also affects the dispersion or accumulation of cold air. Gullies and concave slopes are frost-prone areas compared to convex sites, while the dispersion or accumulation of cold air on flat sites is dependent upon whether the surrounding topography allows the air to drain off the site.

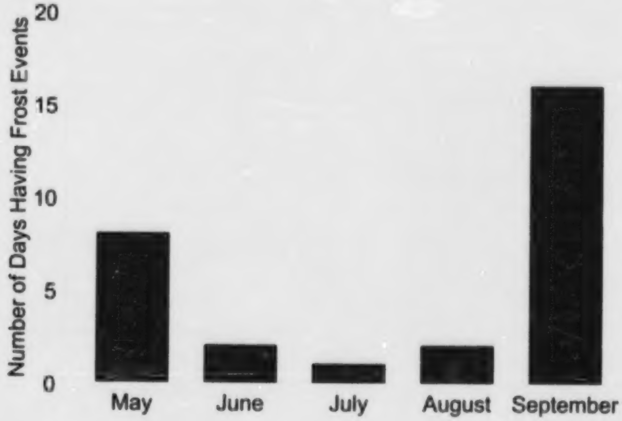
Radiative frosts occur during the summer on calm and clear nights when the ground surface cools due to the transfer of thermal energy into the air. The rate at which the soil surface cools is determined by the difference between the rate of heat loss from the ground to the sky and the rate at which heat stored in the soil is transferred to the soil surface (Fig. 1.1.1*b*). Heat loss from the ground to the air is dependent upon the concentration of water vapor in the atmosphere. That is, high water vapor concentration in the air causes thermal radiation to be absorbed and radiated back toward the ground, while low water vapor concentration in the air results in thermal radiation being transmitted into the night sky. As a result, the rate of thermal radiation loss from the ground to clear sky is 5–10 times greater than under cloudy conditions and can result in a 4–5°C decrease in minimum air temperature at seedling height, and the same decrease in soil temperature

(Geiger 1980; Stathers 1989). Under clear night sky conditions, the temperature near the soil surface decreases rapidly, and frost occurs near the soil surface (at 5–15 cm) even though the air temperature above the ground (at 1.3 m) is well above the freezing point. Windy conditions can reduce the incidence of frost because wind mixes the radiatively cooled air near the ground with warmer overlying air.

Both the soil type and the amount of vegetation cover also affect the occurrence of radiative frost on a reforestation site. The release of heat from the soil at night is directly affected by the soil composition (i.e., texture, organic matter content, water content, bulk density) (Section 1.2.4). It is important to note that organic soils present conditions for higher frost occurrence because they have a lower capacity to store and transmit heat than mineral soils. Vegetation cover reduces the radiative heat loss from the ground surface, thereby reducing the rate of ground surface cooling at night (Sections 5.4.3, 5.5.2, and 5.6).

Since radiative heat loss occurs all night, daily minimum temperatures occur just before sunrise. The chances for a radiative frost occurring increase at the beginning and end of the growing season when nights are longer. An example of a typical seasonal pattern is shown in Fig. 1.2.3 for a boreal reforestation site. Northern latitude sites without a forest canopy can have frosts throughout the growing season, although a greater frequency of frost occurs in the spring and late summer.

Fig. 1.2.3. The number of days when frost (0 to –8°C) occurred throughout the growing season on open boreal reforestation site (at 1020 m in the central interior of British Columbia, 52° N lat.) (adapted from Grossnickle and Major 1994*b* and unpublished data).



1.2.4 Soil thermal properties

The capacity of a soil to store or transfer heat and maintain a specific soil temperature is determined by the thermal properties of the soil. Soil thermal properties also change, depending upon soil composition, bulk density, and soil water content. The following discussion examines the concepts of thermal conductivity, volumetric heat capacity, and thermal diffusivity, and their influence on changes in soil temperatures for northern latitude reforestation sites.

Thermal conductivity of the soil determines the rate of heat transfer through a soil and is dependent upon the soil temperature gradient. Dry clay and sandy soils have a comparable thermal conductivity (Table 1.2.4). In contrast, a dry peat soil has ~22% of the thermal conductivity of dry clay and sandy soils. Irrespective of soil composition and bulk density, the thermal conductivity of a soil increases as soil water content increases. In other words, as water displaces air in the soil, the capability of heat transfer through the soil also increases. Nevertheless, wet clay and wet peat soils have 72 and 23%, respectively, of the thermal conductivity of a wet sandy soil.

Volumetric heat capacity is the amount of energy required to raise the temperature of a given volume (cm^3) of soil by 1°C. In other words, the larger the volumetric heat capacity, the smaller the change in soil temperature for the same input of energy. Dry clay and sandy soils have a comparable volumetric heat capacity (Table 1.2.4). In contrast, a dry peat soil has ~30% the volumetric heat capacity of dry clay and sandy soils. Water contains approximately 3500 times as much thermal energy as the same volume of air at the same temperature. This means that as the water content of a soil increases, it requires a proportionally greater amount of energy exchange between the atmosphere and the soil surface to increase the temperature of the soil. Conversely, once the soil has reached a certain temperature, any decrease in soil temperature through thermal radiation is slower as the soil water content increases. Organic soils have the highest

Table 1.2.4. Thermal properties of air, water, and various soils.

Material	Thermal conductivity $W\ m^{-1}\ K^{-1}$ (× 1)	Volumetric heat capacity $J\ m^{-3}\ K^{-1}$ (× 10^6)	Thermal diffusivity $m^2\ s^{-1}$ (× 10^{-6})
Still air	0.025	0.0012	20.5
Still water at 4°C	0.57	4.18	0.14
Dry sand	0.30	1.28	0.24
Wet sand	2.20	2.96	0.74
Dry clay	0.25	1.42	0.25
Wet clay	1.58	3.10	0.51
Dry peat	0.06	0.58	0.10
Wet peat	0.50	4.02	0.12

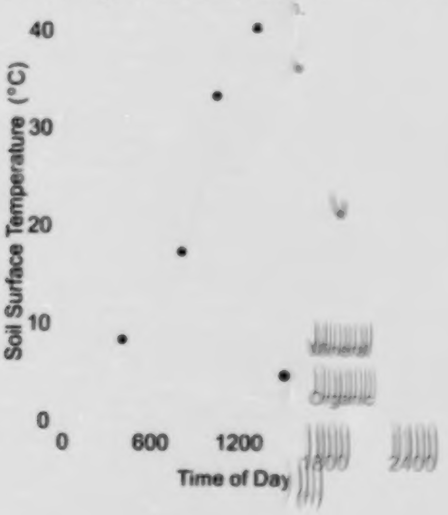
Note: Adapted from Stathers and Spittlehouse 1990.

volumetric heat capacity due to their high water-holding capacity. As a result, wet sand and clay soils have ~75% the volumetric heat capacity of organic soils.

Thermal diffusivity is an expression of the rate at which soil heats up as the result of a thermal gradient (i.e., the ratio of thermal conductivity to volumetric heat capacity). Thus, it determines how rapidly temperature changes occur in the air or through the soil profile (Table 1.2.4). In sandy or clay soils, thermal diffusivity is highest at a soil water content of 10–15%, while thermal diffusivity is low at all water contents in organic soils (Geiger 1980; Stathers and Spittlehouse 1990). Dry soils have lower thermal diffusivity than wet soils because temperature changes are transmitted slowly due to the soil having a low thermal conductivity.

Extreme diurnal temperatures can occur at the soil surface, especially in dry organic soils having very low thermal conductivity. When this occurs, thermal exchanges with the atmosphere are concentrated near the soil surface. Dark organic soils can typically be 10–15°C higher than light-colored soil surfaces (Geiger 1980; Lee et al. 1975). This pattern is depicted on a clear sunny day in midsummer for both a light-gray mineral soil and a dark-brown soil having a high organic matter content (Fig. 1.2.4*a*). Soil surface temperatures of open reforestation sites in the northern latitudes can normally be 2.5–3.0 times greater than soil surfaces under a vegetation cover (Spittlehouse and Stathers 1990), with soil surface temperatures on open sites sometimes reaching into the 40– 50°C range and in certain instances exceeding [illegible] 1972; Nobel and Alexander 1977; Tranquillini [illegible] temperatures, can create stressful microsites for [illegible]

Fig. 1.2.4*a*. Diurnal soil surface temperatures of both [illegible] dark-brown soil having a high organic matter content on an open reforestation site during the middle of July (Grossnickle 1983). Air temperature at 1.5 m ranged from a low of 8°C before dawn to a high of 22°C at 1300 h.



(Section 5.4.4). Organic layers warm and dry out quickly, and do not allow effective heat transfer down into the soil, which can result in high soil surface temperatures but low root zone temperatures.

Moist mineral soils generally have the highest thermal diffusivity, as solar energy absorbed at the soil surface penetrates into the soil profile, resulting in warmer soil temperatures deeper in the profile. Organic soils have the lowest thermal diffusivity values, which results in poor heat transfer to underlying soil layers (Table 1.2.4). This phenomenon causes a reduction in growing season soil temperatures on reforestation sites when there is an organic layer overlying the mineral soil (Fig. 1.2.4*b*). These low thermal diffusivity values for dry or moist organic soils means that an organic surface layer is an effective barrier for limiting heat penetration down into the soil profile (Geiger 1980; Stathers and Spittlehouse 1990).

Saturated peat-based soils have a very low thermal diffusivity, as they warm more slowly due to a high volumetric heat capacity, and because more energy is being lost through latent heat of evaporation (Stathers and Spittlehouse 1990). For example, undrained boreal peatland soils have lower growing season soil temperatures than drained peatland soils (Fig. 1.2.4*c*). In this example, the saturated soil had only 64% of the heat accumulation that a drained soil had throughout the growing season. Thus, northern latitude reforestation sites that have

Fig. 1.2.4b. The number of degree days [illegible]

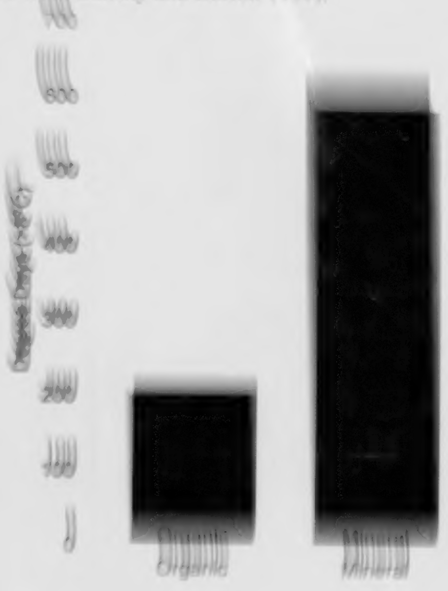
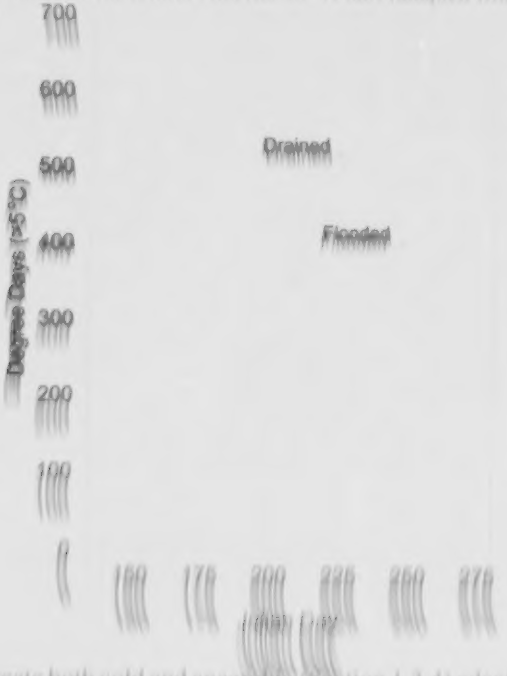


Fig. 1.2.4c. The number of degree days (i.e., summing of mean daily temperatures >5°C) of soil temperature (at –10 cm) that occurred throughout the growing season on a drained and flooded site (in central Alberta, 56° N lat.) (adapted from Lieffers and Rothwell 1987).



saturated soils create both cold and anaerobic (Section 1.3.1) edaphic conditions, which affect seedling performance (Section 1.3.2.2) and influence silvicultural practices that are implemented (Section 5.4.5).

1.2.5 Frost heaving

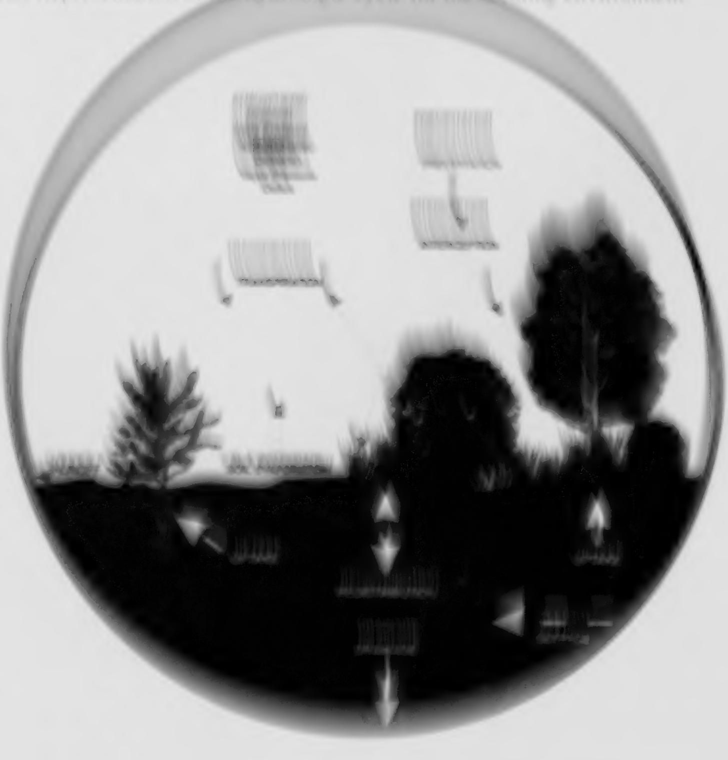
Frost heaving occurs when intermittent freezing and thawing of the soil, without snow cover, causes the heaving of plants from the soil (Goulet 1995). As water freezes near the soil surface, beginning in the larger pores, ice lenses form in the soil and lift both the surface soil and newly established plants. The downward progress of freezing in the soil is slow due to the heat of fusion that is released when ice is formed. As a result, the development of ice lenses continues if more water comes up through capillary action from further down in the soil profile. When these ice lenses, or needles, grow out of the ground in large numbers, they look like a comb and are able to raise plant and soil materials to heights of several centimeters (Geiger 1980). When ice thaws in the daytime, the soil settles again, but the plant remains in the frozen position because the entire root system has been pulled upwards. When this heaving process is repeated over a series of nights, the root systems can be exposed up to several centimeters, and this can influence plant performance (Section 5.4.2). In some instances, this frost-heaving process can pop plants completely out of the ground.

Frost heaving occurs in fine-textured soils with a high soil water content and a series of nighttime freezing to daytime thawing events (Orlander et al. 1990). Retention of a vegetation cover prevents the rapid freezing of the soil surface and reduces the chances of frost heaving from occurring (Goulet 1995). A discussion of how frost heaving affects the performance of spruce seedlings and how silvicultural practices can minimize the occurrence of frost heaving is found later in this treatise (Section 5.4.2).

1.3 Hydrologic factors

The hydrologic cycle of a site is made up of water inputs and losses from the soil profile (Fig. 1.3). Inputs occur through precipitation and downslope seepage. Losses occur through interception of rainfall, runoff, redistribution within the soil profile, and drainage off the site. Site factors that affect the soil energy balance (i.e., incoming solar radiation that affects air temperature and relative humidity) also affect water losses that occur through soil evaporation, plus water uptake by vegetation and the transpirational transfer to the atmosphere. An understanding of the hydrologic cycle of northern latitude reforestation sites is critical for successful plantation development. This is due to the fact that the flow of water through the hydrologic cycle affects many of the physiological

Fig. 1.3. Representation of the hydrologic cycle for the seedling environment.



processes of spruce seedlings (Sections 2.1, 3.2, 3.5.2), which in turn has a direct bearing on the field performance of spruce seedlings in relation to silvicultural practices (Sections 5.3, 5.4.1.1, 5.4.1.5, 5.4.4, 5.4.5, 5.4.7, 5.5.3, 5.6).

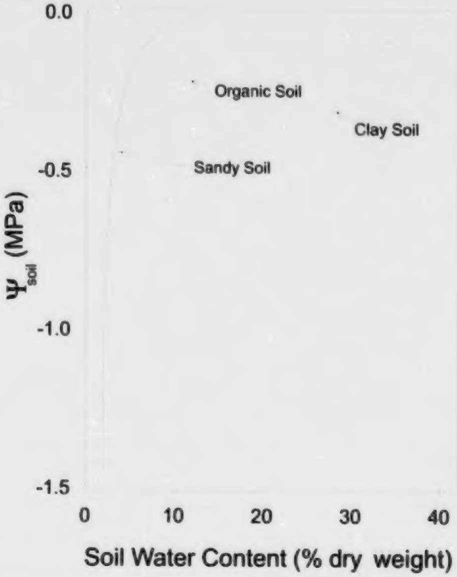
1.3.1 Soil water content

Soil comprises three basic substances or parts: mineral solids, organic matter, and pore spaces containing air or water. The balance between these three parts influences the texture and bulk density of the soil and in turn determines the availability of soil water to seedlings. In addition, the soil water content influences soil thermal properties (Section 1.2.4). The combination of soil water and soil thermal properties can also influence whether seedlings are exposed to frost-heaving events (Section 1.2.5). The following discussion examines how soil characteristics influence the soil water potential as well as the availability of water in northern latitude forest soils.

Amount and plant availability of soil water is dictated largely by the size distribution of individual soil particles, or soil texture. Particle sizes range from 2 to 200 mm for sand and organic matter, and to <2 mm for clay particles. Irregularly shaped pores formed between adjacent soil particles represent 40–60% of the soil volume and can contain both air and water. As water from precipitation and snow-melt infiltrate the soil, these voids become filled with water by capillary action. The relative amount of water that is retained in the upper soil layers as capillary water and the portion that sinks through as gravitational water depend upon the nature of the soil and distribution of pore sizes of the soil structure. Soil pores up to about 10 mm in diameter hold water by capillary action, while coarser soils (pores >60 mm) allow water to pass through rapidly (Hillel 1971). Field capacity of a soil is the water content after gravitational water has percolated through, and all that remains is capillary water. Surface tension forces associated with liquid–air interfaces act to hold water within these voids. These attractive capillary forces create a soil water tension, or soil water potential (Ψ_{soil}).

The drier the soil, the greater the attraction of water to soil particles and the lower or more negative Ψ_{soil} becomes (Kohnke 1968). Water is more tightly bound in smaller pores and thus does not drain because gravity cannot overcome this attraction. Coarse-textured soils, such as those with high sand or organic matter content, have a predominance of large pores that allow water to drain rapidly from the soil profile. Finer-textured mineral soils, higher in clay and silt content than coarse-textured soils, have a greater proportion of smaller pores and thus hold more water against gravity. As a result, water drains rapidly from coarse-textured soils, resulting in a lower Ψ_{soil} than in mineral soils when soils are below saturated conditions (Fig. 1.3.1*a*). Consequently, the lower water storage capacity of coarse textured soils causes rapid drying through greater gravitational drainage of water from the upper portions of the soil. When this phenomenon occurs within the effective rooting zone for newly planted containerized spruce seedlings, it can cause planting stress (Section 5.3).

Fig. 1.3.1*a*. Generalized soil water potential (Ψ_{soil}) curves for sandy, organic, and clay soils over a range of soil water contents.



Soil texture also affects soil water availability through its influence on hydraulic conductivity. The hydraulic conductivity of soil is dependent upon whether the soil is in a saturated or unsaturated condition. Under saturated conditions, water flow through the soil is dependent upon the cross-sectional area of the pores (i.e., conductivity increases to the fourth power of the soil pore radius) (Kohnke 1968). In unsaturated soil conditions, conductivity is dependent upon the size of the pores and on the degree of dryness (i.e., the drier the soil, the smaller the rate of conductivity). Thus, soil hydraulic conductivity is generally higher in very porous soils under saturated conditions, while conductivity under unsaturated soil conditions is generally higher in soils with smaller soil pores.

The flow of liquid water from soil to roots is a function of the Ψ_{soil} gradient between soil and root, and the soil hydraulic conductivity. Root water uptake results in decreased Ψ_{soil} near the root surface. This drop in Ψ_{soil} near the root surface is greater with higher rates of root water uptake. The corresponding reduction in soil water content also results in decreased soil hydraulic conductivity. In coarser-textured soils, the decrease in hydraulic conductivity with a decrease in soil water content is comparatively greater than fine-textured soils due to large pore sizes of coarse-textured soils. To overcome the relatively large reduction in conductivity in these coarse-textured soils, seedlings must be able to tolerate low root and plant water potentials (Ψ) necessary for water uptake (Dosskey and Ballard 1980; Bernier 1992) (Sections 2.1.2, 3.5.2.1, and 5.3).

Soil bulk density also affects the soil pore spaces that can hold water. The compacting of soil increases its bulk density, decreasing the number of large pore spaces, and thereby reducing soil water storage capacity (Kohnke 1968). Initially, increasing the number of micropores in compacted soils can promote greater unsaturated flow of water into drier regions of the soil through capillary water movement. However, further increases in the soil bulk density, causing a reduction in the size of soil pores, results in water being more tightly bound within the smaller soil pores as well as the water-holding capacity of the soil being diminished. Higher soil bulk density means that water is tightly bound in smaller pores that are less easily drained by gravity or readily accessed by plant roots. Thus, soil compaction can create soil water conditions that are characteristic of finer-textured soils. It can also reduce the number of air-filled pores and thereby create anaerobic conditions.

Forest soils become anaerobic whenever the soil oxygen concentration is reduced by an elevated water table and when an impermeable subsoil or flooding reduces soil aeration (Kozlowski 1982). Air-filled pore spaces are eliminated in stagnant water, causing root and shoot growth to decline markedly, even in flood-tolerant species. The diffusion coefficient of oxygen in air is 0.205 $cm^{-2}\ s^{-1}$, while in waterlogged soils oxygen diffusion decreases to $1 \times 10^{-5}\ cm^2\ s^{-1}$. As a result, water logged soils can quickly become devoid of oxygen needed for seedlings to function properly. Water itself is not damaging, and trees can be grown in aerated, nutrient-rich water. Roots are damaged in flooded soils from the lack of oxygen, which causes roots to produce ethylene and toxic substances (Kozlowski 1982), and this has a direct effect on the performance of spruce seedlings (Section 3.5.2.2). Harvesting practices can affect the water table of low-lying boreal forest sites. For example, clear-cutting on wetland northern latitude sites can cause the water table to rise into the surface layers where it can come in contact with the root systems of recently planted seedlings (Dubé et al. 1995).

Removal of the forest canopy alters the hydrologic cycle of the reforestation site. Trees intercept precipitation that, depending upon climate and canopy architecture, may eventually reach the soil or may evaporate from the forest canopy. In conifer forests, the forest canopy can intercept 20–85% of the rainfall before it reaches the ground (Benecke 1976; Geiger 1980), while hardwood-dominated forest canopies intercept from 10 to 50% of total rainfall (Benecke 1976). The wide range in canopy interception values is due, in part, to species shoot structure and leaf characteristics. Removal of the forest canopy can increase the amount of precipitation (up to 15–50% more) reaching the soil surface (Hungerford 1979; Jansson 1987) (Fig. 1.3.1*b*). It must also be recognized that interception is proportionally greater when amounts of precipitation are small, because of the quantity required to wet the crown, and interception decreases, as a percent of the total precipitation event, as the rain intensity increases.

Tree removal also results in lower total stand transpiration rates. The leaf area of a forested stand is much higher than shrubs and herbs that occupy a clear-cut site (Hornung and Newson 1986), and this reduces site evapotranspiration (Miller 1983). As a result, recently harvested clear-cut sites can have higher Ψ_{soil} than the surrounding forest (Fig. 1.3.1*c*). In low-lying areas, there may be a rise

Fig. 1.3.1*b*. Precipitation measured on the forest floor throughout the growing season for a northern latitude location (Tanna River, Alaska, 64° N lat.) in a mature spruce forest and a clear-cut site (adapted from Viereck et al. 1993).

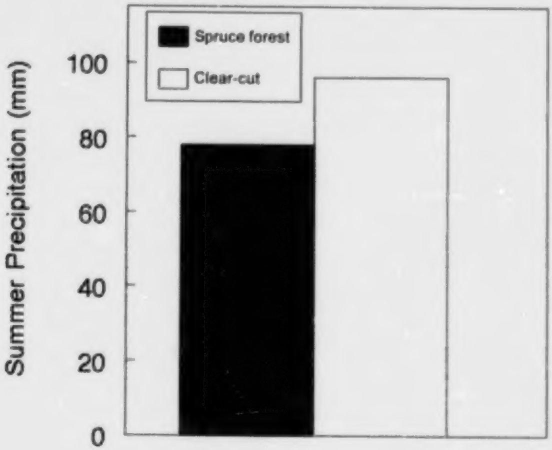
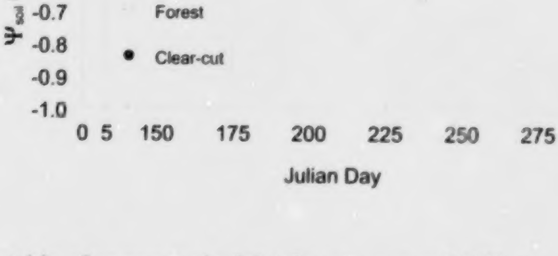


Fig. 1.3.1*c*. Change in soil water potential (Ψ_{soil} at 15 cm in depth) throughout the growing season in a recent clear-cut, with no vegetation control, and in a forested site in the boreal forest (Chapleau, Ont., 47° N lat.) (adapted from Groot et al. 1997).



in the water table after removal of the forest canopy (Williams and Lipscomb 1977). However, the increased soil water on a newly planted reforestation site is usually short-lived. As competing vegetation starts to occupy the site, soil water levels near the soil surface are reduced (Section 5.5.3). Thus, changes in the soil water regime of a reforestation site vary, depending upon factors affecting the hydrologic balance.

1.3.2 Atmospheric humidity

The humidity of the air around a plant is critical because it affects the rates of evaporation of water from the soil surface and the leaves. Atmospheric humidity has a strong effect on the hydrologic cycle of the site through its effect on evapotranspiration processes (Fig. 1.3). This in turn has a direct influence on the water movement through seedlings (Section 2.1.2) and on their gas exchange processes (Section 3.2).

Atmospheric humidity is defined as the amount of water vapor present in a given volume of air, is very strongly temperature dependent, and is expressed as mass per volume. Relative humidity is defined as the ratio of the vapor pressure of unsaturated air to saturated air at the same temperature, and is usually expressed as a percentage. Relative humidity only provides information about the absolute humidity if the temperature is also known.

Water vapor in a given volume of air has a partial pressure (e) that is dependent on the amount of water vapor and its temperature. Saturation water vapor pressure (e_s) is the partial pressure of water vapor in air saturated at a given temperature, and is dependent on temperature alone. When the air becomes saturated with water vapor, e_s is identical to the vapor pressure of water and net evaporation ceases. Ambient vapor pressure (e_a) is defined as the partial pressure of water vapor in unsaturated air. Vapor pressure deficit (VPD) is the difference between the e_s and e_a at a given temperature.

The VPD can be viewed as an indicator of the drying power of the air. The VPD of the air is the driving force that cycles water back into the atmosphere within the hydrologic cycle through evaporation of water from the soil and transpiration from plants (Fig. 1.3). Vapor pressure deficit changes in an interdependent fashion with changes in both air temperature and relative humidity (Fig. 1.3.2*a*). The gas exchange processes of spruce seedlings are directly affected by the VPD of the air (Section 3.2).

The temperature at which water begins to condense out of saturated air is called the dew point. This occurs when the air is cooled to the point that e_s equals e_a and condensation occurs. The dew point is directly related to the amount of water vapor in a volume of moist air. Dew usually occurs on seedlings in the field during spring and summer in the early morning hours when humid air comes into contact with a cooler surface, such as spruce needles (i.e., due to nighttime sensible heat loss), causing condensation to occur. In certain instances, this may be important in creating a favorable water balance in spruce seedlings (Section 2.1.2).

As the relative humidity of the air decreases below 100%, its affinity for water increases dramatically, thereby causing a very rapid drop in the atmospheric water potential. For example, at an air temperature of 20°C, as relative humidity decreases from 100 to 95%, atmospheric water potential can decline to an equivalent of approximately –7 MPa (Fig. 1.3.2*b*). With further decreases in the

Fig. 1.3.2*a*. Changes in vapor pressure deficit of the air as a function of air temperature and relative humidity (RH).

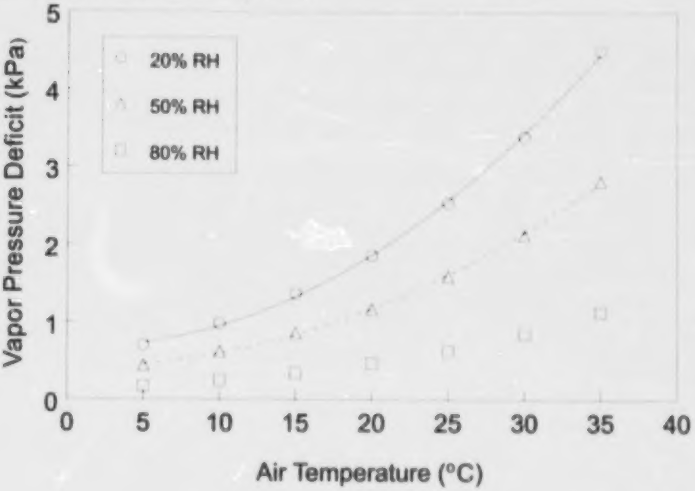
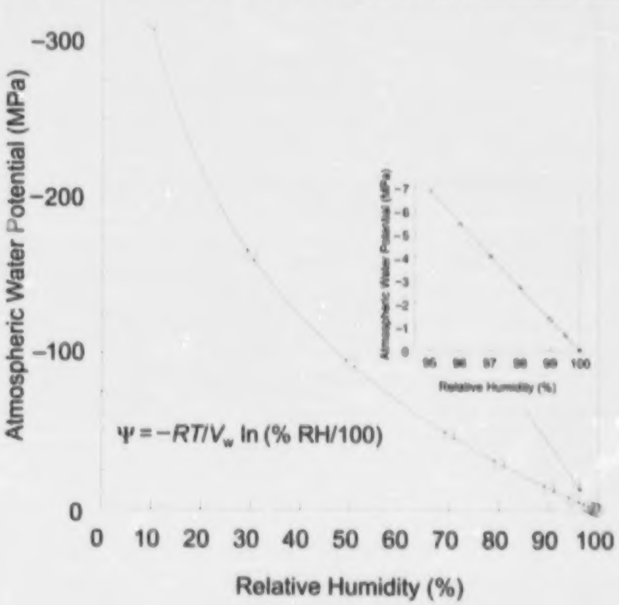


Fig. 1.3.2*b*. The relationship between atmospheric water potential (at 20°C) to relative humidity. Insert figure presents a close-up of this relationship between 100 and 95% relative humidity. Parameters in the equation are defined as the following: Ψ is the atmospheric water potential, R is the gas constant (J mol^{-1} K^{-1}), T is the absolute temperature (K), V_w is the molar volume of water, and RH is the relative humidity.



relative humidity to 70, 50, and 10%, atmospheric water potential can be an equivalent of approximately –30, –94, and –311 MPa, respectively. The resulting effect is a very steep water potential gradient from the plant to the air, which starts the process of water moving from a location of higher water potential (i.e., the soil) through the seedling into the air, through the soil–plant–air continuum (Section 2.1.2).

The gradient between the atmospheric demand for water and soil water availability is also one of the causes of evaporation from the soil surface on reforestation sites. Removal of the forest canopy, through clear-cutting, affects the microsite temperature around seedlings (Section 1.2). This canopy removal can cause a reduction in the relative humidity (Reynolds et al. 1997) or an increase in VPD (Marsden et al. 1996). Clear-cutting can increase site evapotranspiration throughout the growing season, compared to a mature white spruce forest (Viereck et al. 1993). For example, on a sunny, summer day during the growing season, VPD was much higher on a clear-cut site than in a forested stand throughout the entire day (Fig. 1.3.2*c*). As air temperatures increased during the middle of the day, relative humidity declined, and VPD increased with a greater change on the clear-cut compared to the forested site. Thereafter, as temperature declined in the late afternoon, VPD decreased until both sites had similar VPD conditions late in the day. Removal of the forest canopy has a direct effect on relative humidity and VPD, and thus, the overall hydrologic cycle of a reforestation site.

During the growing season, northern latitude reforestation sites have a range of VPD (Fig. 1.3.2*d*). In this example, this site has low VPD (<2 kPa) on 61% of

Fig. 1.3.2*c*. Diurnal change in vapor pressure deficit (VPD) of the air at seedling height for a clear-cut and forested site in the boreal forest (Chapleau, Ont., 47° N lat.) (adapted from Groot et al. 1997).

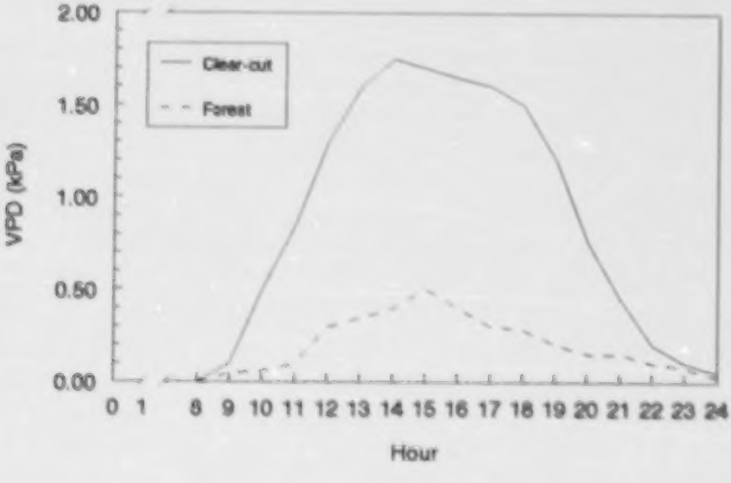
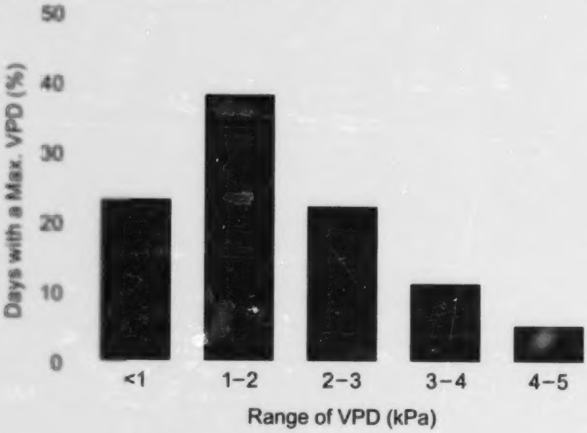


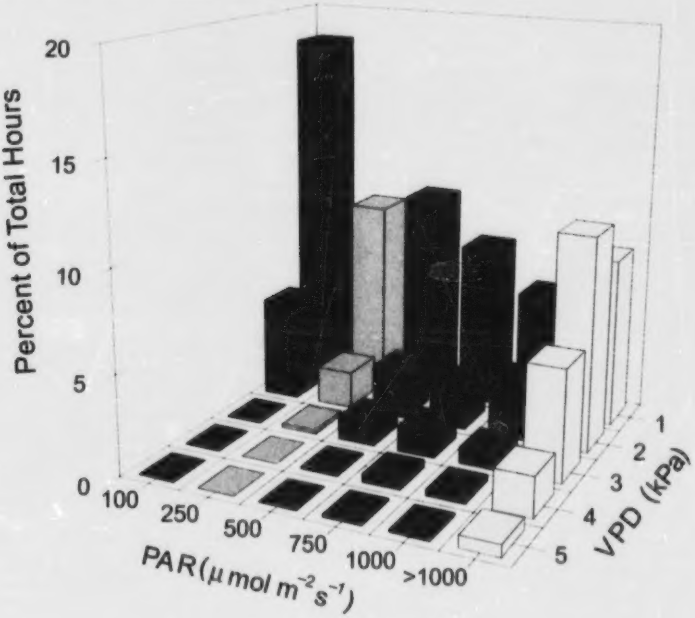
Fig. 1.3.2*d*. The percentage of days where maximum vapor pressure deficit (VPD) levels fit within defined ranges of VPD throughout the growing season (June through September) on a boreal reforestation site (Williams Lake, B.C., 52° N lat.) (adapted from Grossnickle and Major 1994*b*).



the days and moderate VPD (2–3 kPa) on 22% of the days during the growing season. Only 16% of the days had high (>3 kPa) VPD. This range of VPD is fairly typical for northern latitude reforestation sites where spruce seedlings are planted, depending upon the location and precipitation patterns during the growing season. High VPD conditions can occur during the growing season on sites located in the southern regions of the boreal forest and in years when there are extended periods without summer rains (Larsen 1980). In addition, high VPD conditions regularly occur during the summer in subalpine forests of the Rocky Mountains (Day 1963; Kaufmann 1982*a*). However, Smith (1985) concluded that the physiological response of subalpine conifer species to air dryness is of secondary importance during most summers, compared to other potentially limiting environmental factors (i.e., suboptimal air and soil temperatures, low soil water). These findings indicate that VPD can be a contributing factor, although not always the dominant factor, in limiting spruce seedling performance.

Reforestation sites present conditions where seedlings are exposed to continual changes in both light and VPD during the growing season. Both light and VPD continually change in a dynamic and interrelated fashion throughout each day. In this example, the reforestation site is exposed to a wide range of light conditions during the growing season, although VPD remains low (Fig. 1.3.2*e*). High VPD levels are usually accompanied by high light levels. Continually changing atmospheric conditions have a direct bearing on the gas exchange process of spruce species (Sections 3.1, 3.2, and 3.8). These are the primary environmental parameters that influence the gas exchange processes of conifer species during the growing season when soil temperature and water are not limiting (Kaufmann 1982*a*; Landsberg 1986).

Fig. 1.3.2*e*. The percentage of daylight hours for the combination of vapor pressure deficit (VPD) and photosynthetically active radiation (PAR) that occur throughout the growing season (June through September) on a boreal reforestation site (Williams Lake, B.C., 52° N lat.) (Grossnickle, unreported data).



1.4 Wind

Opening up a forest stand through clear-cutting increases air movement across the reforestation site (Geiger 1980; Spittlehouse and Stathers 1990). However, the direct effect of clear-cutting on air flow patterns is variable and is dependent upon topography, previous forest structure, and size and shape of the reforestation site. In one example, a mature white spruce forest had only 4% (Fig. 1.4*a*), while a deciduous forest had only 8–18% of the surface winds within the stand that occurred on a clear-cut site (Viereck et al. 1993). Consequently, open reforestation sites can create conditions for the occurrence of greater wind speeds.

Wind speeds decrease downward within a vegetation cover and can prevent the advective transfer of thermal radiation from the soil surface. This occurs because the presence of a vegetation cover, with a defined roughness length (i.e., a measure of the frictional ability of the surface to absorb the momentum from air moving over it), raises the effective surface above the soil (Ethrington 1982). In general, the roughness length increases with height of the vegetation (e.g., approximate roughness lengths are 0.1 cm for a soil surface, 0.6–4.0 cm for short-grass, 4–10 cm for long-grass, 20 cm for shrubs). The roughness length is not usually at the top of the plant canopy, rather it is further down within the canopy.

Fig. 1.4*a*. Wind measured throughout the growing season for a northern latitude location (Tanna River, Alaska, 64° N lat.) in a mature spruce forest and a clear-cut site (adapted from Viereck et al. 1993).

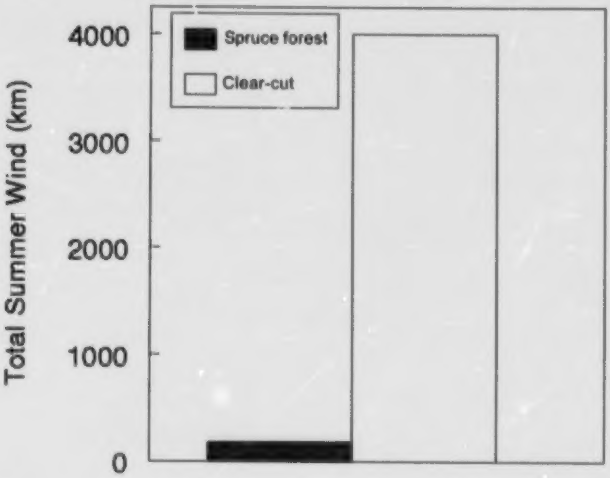
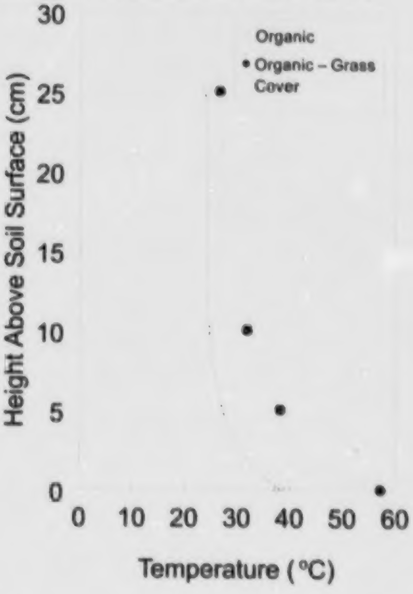


Fig. 1.4*b*. Midday near-soil surface air temperature profile, during the midsummer, on an open reforestation site for an organic soil, with or without a light grass cover (i.e., ~40 cm tall) (adapted from Grossnickle and Reid 1984*a*).



This displacement height is where the wind speed profile extrapolates to zero because the momentum of the wind is being absorbed by the vegetation. The displacement height is not stable, but changes in a dynamic fashion due to the structure of the vegetation canopy and varying wind speeds. This is why a partially open vegetation cover can trap heat a[illegible] wind currents or thermal transfer of radiation e[illegible] up, thereby causing temperatures to rise to ext[illegible] surface (Geiger 1980). An example of this phe[illegible] where a light cover of grass can cause an increase in near-soil surface air temperatures, with the soil surface temperature almost 20°C higher than a similar soil surface without a grass cover. The presence of competition on a reforestation site can in certain instances limit winds along the soil surface and cause an increase in the near-soil surface air temperatures. These high near-soil surface air temperatures can create stressful microsites (Section 5.4.4) that affect the physiological performance of spruce seedlings (Section 3.3.2).

1.5 Soil nutrition

1.5.1 Mineral nutrients in the soil

Soil nutrients that are necessary for the health and growth of seedlings occur in the soil in both dissolved and chemically bound forms. Only a fraction of soil nutrients (<0.2%) are dissolved in the soil water. The majority of the remaining elements (almost 98%) are bound, or contained in organic detritus, humus, minerals, and relatively insoluble inorganic compounds. Nutrients in these forms become available only as a result of weathering and mineralization of humus. The remaining soil nutrients (2% of the total) are adsorbed on soil colloids, or particles.

Most soil particles (i.e., colloidal clays and humic substances) have a negative charge that attracts mineral nutrients and bind them reversibly. Thus, they act as ion exchangers. The exchange capacity o[illegible] charge, and this allows them to preferentially retain mineral cations. There are also a few positively charged sites where mineral ions can be attracted. As a rule, more highly charged mineral ions have a higher attraction to these exchange sites (e.g., $H^+ > Ca^{+2} > Mg^{+2} > K^+ >$ N[illegible] NO_3^- for anions). If ions are added to or withdrawn from the soil solution, then ions that are attracted more strongly to the soil particles displace ions with a lower attraction. The binding of mineral ions to [illegible] of soil solution and prevents them from being leached from the soil, and also allows only a low level of ions in solution. This process controls the exchange of mineral ions and ensures a continual supply of nutrient ions that can be readily available for absorption by the seedling root system.

This ion exchange process and the equilibrium of ions in soils is strongly influenced by the concentration of hydrogen ions (pH) in the soil solution. The pH of a soil is a measure of the hydrogen ion ([illegible]) concentration expressed as a logarithmic scale. Mineral ions come into and go out of solution as soil pH changes (i.e., based on the proportion of H^+ ions that occupy negatively charged sites); thus pH is considered the controlling variable of soil nutrient availability (Table 1.5.1). As a result, the availability of various mineral ions to spruce seedlings for absorption changes as soil pH changes. As well, the level of mineral ions lost from the soil through leaching changes as soil pH changes. Northern latitude forest soils can have pH levels that range from [illegible] (Brand et al. 1986; [illegible]). [illegible] ions of spruce, compared to pines or hardwoods, have a greater [illegible] effect on reducing the pH in the upper portions of the soil profile (Binkley and Valentine 1991). The pH of these soils at any given time is influenced by time of year, especially due to precipitation patterns, and also varies, depending on the structural makeup of the different soil horizons. Factors that affect soil formation change as the soil pH changes. For example, chemical weathering increases as pH decreases; humification is highest within the pH range of 5–7; and soil biotic activity increases to a pH of 7.2, declining with further increases of pH. Atmospheric inputs of protons, N, and S from anthropogenic sources may also be leading to accelerated soil acidification in northern latitude forests (Matzner 1992). Changes in these factors have a long-term influence on the availability of mineral ions.

Table 1.5.1. The range in pH that allows for the maximum availability of mineral nutrients in the soil solution.

Mineral nutrient	*Maximum availability pH range*
N	5.5–8.0
P	6.0–7.0
K	7.5
Ca	5.5–8.0
Mg	5.5–8.0
Mn	Decreases at pH > 5.0
Al	Decreases at pH > 5.0 and is unavailable beyond 5.5
Fe	Decreases at pH > 5.0
B	4.0–7.0
Cu	5.0–5.5
Zn	5.0–5.5
S	5.5–8.0
Mo	Increases at pH > 5.0

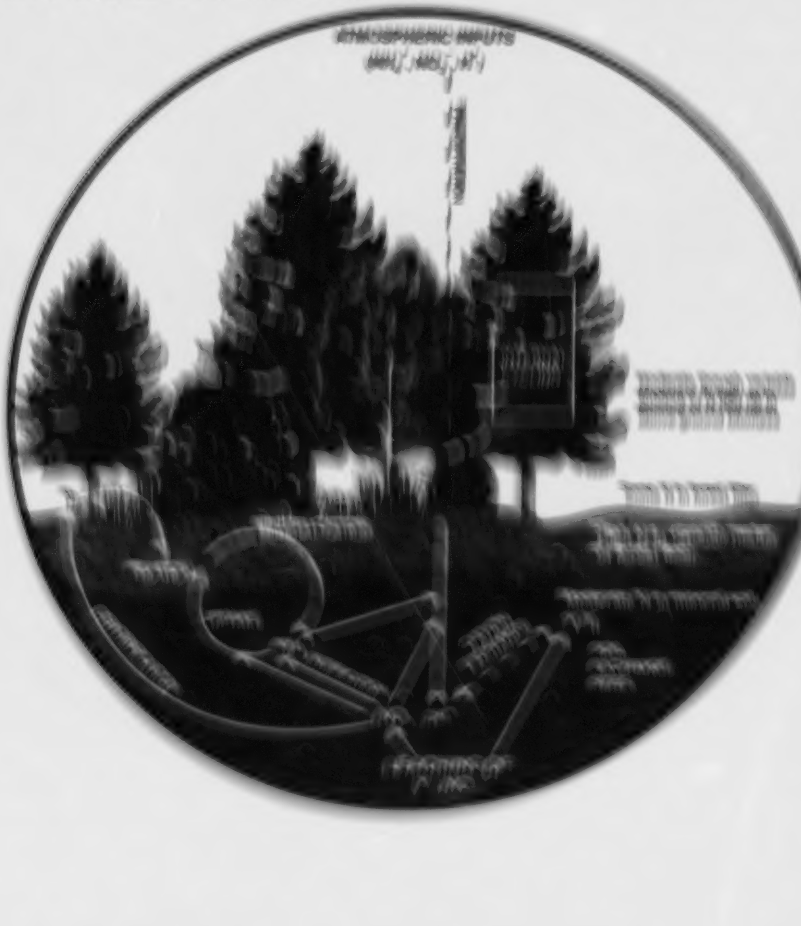
Note: Adapted from Etherington (1982) and Landis (1985).

1.5.2 Nutrient cycling

The circulation of nutrients through the forest is an important part of the ecosystem. All nutrients have three major cycles (shown for N in Fig. 1.5.2a): geochemical, biogeochemical, and internal cycling. The geochemical cycle involves atmospheric and soil weathering inputs of the [illegible] of nutrients through [illegible]. The biogeochemical cycle involves the [illegible] of nutrients by trees from the soil and their return to the soil via [illegible] [illegible]. Internal cycling [illegible] [illegible] plants. These three nutrient cycles affect where, and in what amounts, various nutrients accumulate within the northern latitude forest ecosystem.

Each mineral element has a unique biogeochemical cycle (Mengel and Kirkby 1982; Binkley 1986). Cycling of individual nutrients varies in complexity and is inextricably linked to the H^+ budget of the ecosystem, as pH is

Fig. 1.5.2a. The nitrogen (N) cycle and locations of N storage within the temperate and northern latitude forest ecosystems. Double vertical lines represent exchange sites and Y^+ represents other mineral cations.



important to the form, solubility (Table 1.5.1), and plant availability of nutrients, microbial activity, and root function. Only nitrogen cycling is considered here in detail because, after carbon, hydrogen, and oxygen, it is the most abundant element in plants, in terms of quantity. Evergreen foliage contains 1–2% N, and [illegible] and roots 0.5–1% N (Larcher 1995). Also, natural stands of spruce [illegible] in N at a greater rate than other macronutrients. For example, [illegible] As a result, N is commonly the most limiting nutrient in forest ecosystems [illegible] and specifically in northern latitude forests (Van Cleve et al. [illegible]).

The primary input of N into the forest ecosystem is through the atmosphere, as N does not occur naturally in parent material (Fig. 1.5.2a). It is estimated that between 0.1 and 1.0% of the soil N budget accrues as atmospheric inputs within the northern latitude forest ecosystem on a yearly basis (reviewed by Weetman and Webber 1972; Krause et al. 1978). In areas of eastern North America and throughout Northern Europe, greater atmospheric inputs of N can occur from anthropogenic sources. For example, in the northeastern region of the United States, running from east to west, N deposition can range from 2.5 to 16.4 kg ha^{-1} yr^{-1} within spruce–fir forests (Friedland et al. 1991), while N deposition can range from 1 to 27 kg ha^{-1} yr^{-1} from northern Sweden to central Europe (Högberg et al. 1998) and up to 23 kg ha^{-1} yr^{-1} in Sitka spruce forests of the United Kingdom (Fowler et al. 1989). Nitrogen also enters the nutrient cycle through N fixation. Nitrogen fixation occurs through free living organisms (i.e., bacteria and blue-green algae), while other organisms (i.e., *Rhizobium* and *Frankia*) form symbiotic associations with the roots of higher plants (e.g., *Lupinus* spp., *Alnus* spp.). Nitrogen fixation is a biological process; its activity is optimal at 20–30°C and [illegible] to a halt at soil temperatures near 0°C. As a result, the rate of N fixation in [illegible] (Larcher 1995).

Nutrients within the forest ecosystem are located in [illegible] (1) aboveground [illegible] (2) ground cover vegetation, (3) forest floor and organic soil layers, and (4) mineral soil (Fig. 1.5.2a). In northern latitude forest ecosystems, the forest floor and organic soil layers and mineral soil are the main storage compartments of nutrient reserves. In a boreal forest dominated by Norway spruce, the distribution of N throughout the ecosystem was [illegible] in the aerial biomass, [illegible] in the litter on the soil surface, and [illegible] within the soil (Nihlgard 1972). In black spruce boreal forests, the distribution of N ranges from ~10 to 20% in tree biomass, ~30–50% in the organic matter of the forest floor, and ~10–40% in the mineral soil (Weetman and Webber 1972; Weetman and Algar 1983; Morris 1997). Other work has also indicated that the main source of available N in boreal forest soils are found within the soil surface organic matter and turnover of small roots (Keenan 1986), rather than the subsurface fine-textured mineral layers that have low organic matter content (McAlister 1982). The forest floor and organic soil layers of northern latitude forest ecosystems contain 1.5–7.6

times the amount of N found in the aboveground tree biomass (Krause et al. 1978). The decomposition rate of the organic soil layers is very slow, and as a result, the mean residence time (i.e., turnover time) of N in northern latitude forest floors is estimated at 230 years (Cole and Rapp 1981). This is due to the cold soil conditions found in northern latitude forests, which causes the retention of a large long-term reservoir of N within the organic layer of the forest floor.

The majority of N in the forest floor and organic soil layers of northern latitude forests is chemically bound and not available to plants unless made available through mineralization and nitrification processes. If proper soil environmental conditions occur, bacterial decomposition of N-containing organic matter causes NH_4^+ to be released (Fig. 1.5.2*a*). Soil temperature, soil water content, and chemistry of the organic matter are the primary variables that affect the N cycle (Vitousek and Melillo 1979). During the mineralization and nitrification processes, this NH_4^+ can either be taken up by microbes or plants, or be oxidized by specialized autotrophic bacteria and changed into NO_3^-. The lack of a significant soil anion exchange capacity renders NO_3^- mobile and more susceptible to leaching than NH_4^+, but this also increases its plant availability. Mobile NO_3^- can be taken up by plants and microorganisms, or leached through the soil accompanied by cations displaced by hydrogen ions on the cation exchange sites in the soil. However, losses of site N through leaching are estimated to be only up to 0.2% of the N budget of a northern latitude forest ecosystem (reviewed by Weetman and Webber 1972; Krause et al. 1978). Losses of site N can also occur through the denitrification process, where NO_3^- is converted to N_2 gas by bacteria.

In spruce-dominated boreal forests, N mineralization and nitrification processes are low to undetectable within the forest floor and surface mineral soils (Klingensmith and Van Cleve 1993). The low release rate of N within boreal forest soils is due to low soil temperatures, limiting the rate of organic matter decomposition by soil microorganisms (Waring and Schlesinger 1985; Flanagan and Van Cleve 1983; Van Cleve et al. 1981; 1993). Poor soil aeration (i.e., high water table) can also limit organic matter decomposition and subsequent N availability (Flanagan and Van Cleve 1983; Lieffers and Macdonald 1990). For example, a lowland black spruce site was found to have 82% of site N tied up in the organic soil horizons (Morris 1997). It is this low level of biological activity within the forest floor of the northern latitude forest ecosystem that limits the release of all nutrients and reduces long-term stand productivity.

Low mineralization and nitrification activity within northern latitude forest ecosystems dominated by spruce species affects total N supply. As a result of this low level of activity, only 0.6–1% of site available N is fixed annually into plant biomass, and 0.4–1% is annually returned to the soil with litter fall (Nihlgard 1972; Krause et al. 1978). The 9–15% of N that is tied up in tree biomass goes through a seasonal internal cycling process which is dependent upon the spruce species seasonal growth patterns (Section 3.6.1). The low N cycling between the trees and the soil system reduces leaching losses of N, and if any N leaching occurs, it is confined to the nongrowing season (Vitousek 1983). In addition, the annual loss of N through denitrification is small, being only 1–3 kg ha^{-1} yr^{-1} from mature Sitka spruce plantations (Dutch and Ineson 1990). Thus, the forest floor of an undisturbed northern latitude forest ecosystem represents a large passive nutrient pool predominating over a small active pool of nutrients being utilized by the vegetation.

There is recent evidence that organic N is absorbed by plants growing in infertile and (or) highly organic soils. Pine species growing in infertile soils of northern forests produce litter with high concentrations of phenols. This strongly influences the release of dissolved organic N into the soil (Northup et al. 1995). The dissolved organic N then diffuses to plant roots or mycorrhizal fungi and is absorbed into the plant. This is regarded as a possible mechanism by which plants can short-circuit the mineralization step of the N cycle and readily access N from the pool of organic N found in the organic matter of the forest floor (Chapin 1995). Further work is required to substantiate whether this is an integral mechanism of the N cycle for spruce species within temperate and boreal forest ecosystems.

Harvesting a forested stand through clear-cutting alters the N cycle of a temperate or boreal forest ecosystem in a number of ways. First, a certain portion of the site N budget is removed within the trees that are harvested. The amount of N lost from the overall N cycle is dependent upon the harvesting practice. Harvesting of just the tree stems of a spruce forested stand removes only 1.5–4% of the N budget, while full tree harvesting removes from 11 to 19% of the N budget (Weetman and Webber 1972; Weetman and Algar 1983). In a black spruce forest, between 7 and 21% of the N budget is reported to be in harvestable timber (Morris 1997). Standard logging practices do not remove enough of the nutrient pool to cause a reduction in growth during the second rotation of trees (Weetman and Weber 1972). Atmospheric inputs over the expected length of the next forest rotation, a minimum of 50 years, more than make up for nutrient losses that occur due to stem removal logging practices. Also, just after clear-cutting there is a period of increased nutrient availability in the soil system. This availability is due to reduced site nutrient uptake, an increased rate of organic matter decomposition, and an increased quantity of logging slash to be decomposed by the soil microorganisms (Keenan and Kimmins 1993).

By removing the forest canopy during clear-cutting, the reforestation site nutrient cycle is also indirectly affected by changing the soil energy budget (Section 1.2). If the site has a readily available source of carbon, this in combination with an increased soil energy balance can stimulate the site microbial population to cause decomposition of the organic matter and the release of nutrients into the available soil pool (Vitousek et al. 1979; Chapin 1983). In northern latitude forest sites, the increase in forest floor soil temperatures after clear-cutting is considered the principle environmental factor that is responsible for increased N mineralization (Van Cleve et al. 1993). Increased mineralization and nitrification after clear-cutting have been frequently reported, the extent varying with climate, soil conditions, and degree of disturbance (Kimmins and Feller 1976; Krause 1982; Vitousek et al. 1982; Krause and Ramlal 1987; Munson et al. 1993) (Fig. 1.5.2*b*). Due to this phenomenon, recently clear-cut sites in the northern latitude forest are often considered to be "nitrogen saturated" because mineralization exceeds initial nutrient uptake capacity of plants and microorganisms (Staaf and Olsson 1994). Just after clear-cutting, P levels can also double, increasing the availability of this ion within the soil (Krause and Ramlal 1987).

After forest disturbances such as harvesting, the mineralization process causes the inorganic nitrogen source available in forest soils to change from predominantly NH_4^+ to NO_3^- (Vitousek et al. 1979; Jobidon et al. 1989; Lavoie et al. 1992) (Fig. 1.5.2*b*), with greater amounts of available N found in the organic surface layers (Fig. 1.5.2*c*). This shift to NO_3^- in the soil solution can promote the leaching of other cations from the soil solution (Likens et al. 1970). Some of this NO_3^- is also lost through denitrification, a process that can increase dramatically after forest disturbance. Denitrification has been reported to be 10 times greater on clear-cut sites than in mature Sitka spruce plantations (Dutch and Ineson 1990). Nutrients such as N, which have existed as a frozen site asset within the forested stand, are available to contribute to development of the new forest stand, or are lost from the ecosystem through denitrification or leaching processes. Thus, any type of harvesting practice that removes the forest canopy or causes a soil disturbance and alters the soil surface environment, can significantly alter the N cycle.

Increased N mineralization after forest disturbance alters the rate of organic matter decomposition, increases the availability of soil nutrients, and promotes

Fig. 1.5.2*b*. Average seasonal estimates nitrogen production for a northern latitude location (Tanna River, Alaska, 64° N lat.) in a mature spruce forest and a clear-cut site (adapted from VanCleve et al. 1993).

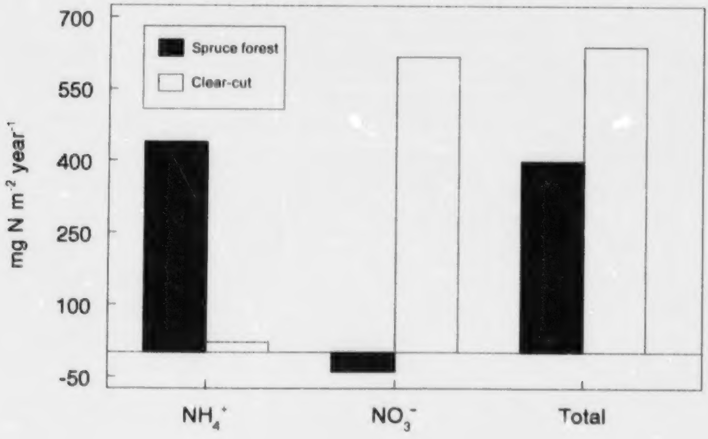
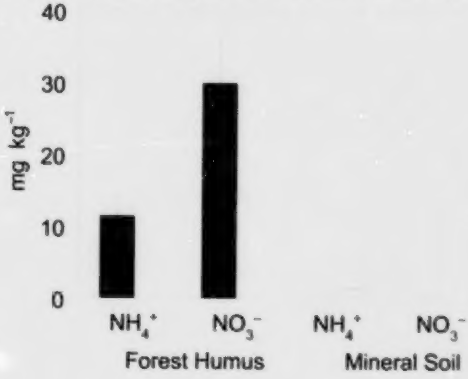


Fig. 1.5.2c. The inorganic NH_4^+ and NO_3^- pools (mean + SE) found in forest humus and surface mineral soil (0–10 cm) 4 years after harvesting on a boreal reforestation site (central Ontario, 46° N lat.) (adapted from Munson et al. 1993).



development of a different type of vegetation complex. As vegetation develops on clear-cuts, nitrification and leaching are reduced due to N uptake from the vegetation on site. This results in very little loss of N from the ecosystem and creates competition for site nutrient resources (Krause et al. 1978; Emmet et al. 1991; Fahey et al. 1991; Örlander et al. 1996). It also demonstrates the dynamic nature of the N cycle on clear-cut sites after spruce seedlings have become established and are undergoing the transition phase of plantation development (Section 5.5.4).

1.5.3 Nutrient availability in the northern latitude forest

The availability of soil nutrients to spruce seedlings varies, depending on the indigenous fertility of the soils found on the reforestation sites. On northern latitude forest sites, the amount of nutrients tied up in aboveground tree biomass has a wide range in variation for N (80–612 kg ha^{-1}), P (10–52 kg ha^{-1}), and K (82–245 kg ha^{-1}) (Krause et al. 1978). The amount of nutrients tied up within the aboveground tree biomass is a reflection of the availability of soil nutrients to the northern latitude forest species. As a result, it is very difficult to define specific levels of forest site nutrient content that are required for adequate growth of spruce seedlings. Minimum soil fertility standards (N at 0.12%, P at 44.8 kg ha^{-1}, K at 145.7 kg ha^{-1}) for sufficient development of forest plantations of white spruce have indicated that this species requires greater soil fertility than other common northern latitude conifer species (Wilde 1966). Ranges of nutrient concentrations required for optimal growth of spruce species are described elsewhere in this treatise (Section 2.3.3).

2 Basic physiological and morphological concepts

This section defines the physiological concepts that are centrally important to the performance of spruce species. Within this section, the areas of water relations, gas exchange, plant nutrition, freezing tolerance, dormancy, and morphological development as they pertain to northern spruce species are explored. The ecophysiological performance of spruce seedlings in response to these basic physiological concepts are the focus of the discussion in Sections 3–5. The intent of this section is to give the readers a clear understanding of the underlying principles for each of these physiological concepts in relation to spruce species. A comprehensive review of each of the basic physiological concepts in relation to plants in general is beyond the scope of this discussion. Readers are referred to Salisbury and Ross (1992) and Kozlowski and Pallardy (1996) for a more in-depth discussion of the physiological processes of plants.

2.1 Water relations

Water is essential for the normal functioning of plants. First, water is an essential component of protoplasm and constitutes 80–90% of the fresh weight of actively growing tissue and ~50% of freshly cut wood. Second, water is a solvent that facilitates movement of materials in and out of cells and throughout various parts of a plant. Third, water is important for photosynthesis and hydrolytic processes. Fourth, water is required for maintenance of turgidity. Thus, plant water relations are critical for the maintenance of a high plant water content and turgor to permit normal physiological processes involved with growth.

This section provides an overview describing the essential principles of water relations that are important in understanding spruce seedling performance. Readers seeking further details on the principles of water relations in plants should refer to Kramer and Boyer (1995).

2.1.1 Water potential

Water potential is designated by the symbol Ψ. It is described in terms of energy, and quantifies the capacity of water to do work in comparison to the work an equal mass of pure water would do (Kozlowski 1982). The Ψ of the water in a seedling is the energy difference between the chemical potential of water and that of free pure water at a standard temperature and pressure (Kramer 1969). The Ψ of free pure water is defined as zero at a fixed height, and the potential in a seedling is decreased by factors that limit its ability to do work (i.e., matrically bound water, negative pressures in the xylem, or osmotically constrained water). Thus, Ψ is the energy status of water within a plant and it ranges from a high of zero, although it usually is a negative number. The more negative the number, the lower the plant Ψ. Water potential is measured as energy per unit volume and is currently reported in megapascals (MPa), although earlier literature used the term bars (10 bars = 1.0 MPa). Knowledge of Ψ in any two plant regions or in the soil and plant indicates which way water moves, as water always moves from an area of high Ψ (i.e., the soil) to an area of lower Ψ (i.e., needles on a seedling).

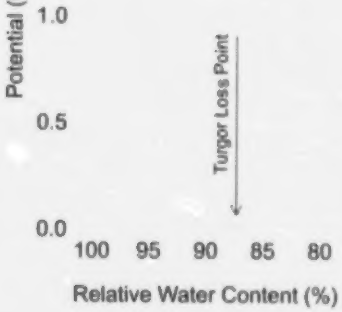
The Ψ within living cells of a plant is primarily made up of turgor pressure potential (Ψ_P) and osmotic potential (Ψ_π). Turgor pressure potential is almost always positive, while osmotic and water potentials are negative. Osmotic potential reflects the concentration of solutes, such as carbohydrates, in the cell. Since Ψ in a plant is always negative, a high Ψ_π indicates a low relative solute concentration. The Ψ of a plant can be defined in terms of the algebraic sum of the main constituent potentials:

$$\Psi = \Psi_P + \Psi_\pi, \text{ or water potential = turgor pressure potential + osmotic potential}$$

The interrelationship between these factors is illustrated by a Höfler diagram (Fig. 2.1.1*a*) which shows the relationship between Ψ, Ψ_P, and Ψ_π as the tissue relative water content changes for spruce. When a seedling is fully turgid, Ψ is zero because Ψ_P is positive and equal to Ψ_π. As seedling Ψ becomes more negative, both Ψ_π and Ψ_P decline. As seedling relative water content decreases, Ψ_P declines until it reaches zero. At this point, a seedling has reached the turgor loss point. This turgor loss point is related to Ψ_π, since Ψ_P is zero.

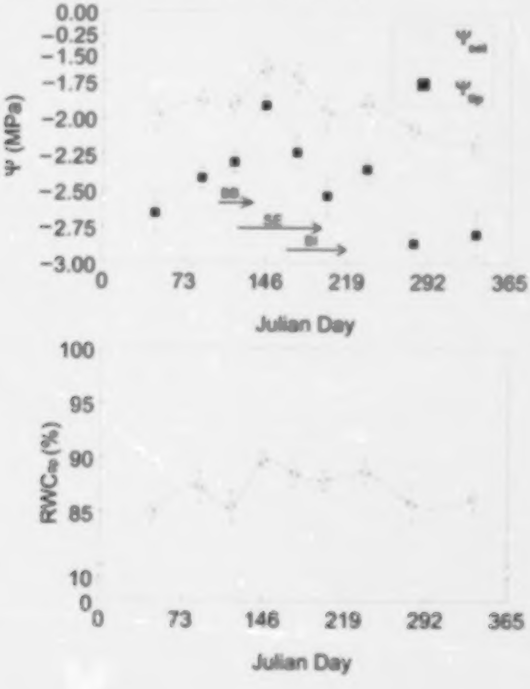
The Ψ_π of a plant is passively lowered by concentrating existing tissue solutes via dehydration. In addition, a plant can lower Ψ_π by increasing the solute content of the cells. This is termed active osmotic adjustment, and it generally involves the uptake, internal production, or transfer of osmotically active substances such as organic ions (i.e., K, Mg, Cl, Ca, NO_3^-), sugars, and amino acids

Fig. 2.1.1*a*. Höfler diagram showing changes in turgor pressure (□), osmotic potential (○), and total water potential (△) in relation to the change in relative water content (RWC = (actual water content / saturated water content) × 100) for white spruce seedlings at the end of the growing season. Turgor pressure potential is positive, while osmotic and total water potentials are negative (adapted from Grossnickle and Blake 1987*a*).



(Tyree and Jarvis 1982). This change in Ψ_π for spruce is partially due to the accumulation of carbohydrates (Zwiazek and Blake 1990*a*; Koppenaal et al. 1991) and soluble sugars (Colombo and Blumwald 1992). A number of studies have found that Ψ_π changes seasonally in spruce species (Grossnickle 1988*b*, 1989; Colombo and Teng 1992; Zine El Abidine et al. 1994*a*; Grossnickle et al. 1996*a*). These seasonal changes in Ψ_π are related to changes in shoot phenology (Fig. 2.1.1*b*). During shoot elongation, Ψ_π of the shoots increases dramatically, reflecting a decrease in solute concentration. It is during this time that spruce species are most susceptible to drought or water stress. When shoot elongation ceases, Ψ_π decreases (solute concentration increases), and the seedling is better able to withstand water stress. The Ψ_π of spruce species continues to decrease during the fall, reaching the lowest point during the winter. Interestingly, this fall seasonal change in Ψ_π parallels the reported seasonal pattern for total soluble sugars in red spruce (Amundson et al. 1992). These findings indicate that spruce species reach their greatest drought and freezing tolerance (Section 3.7.1) during the winter, when they are dormant.

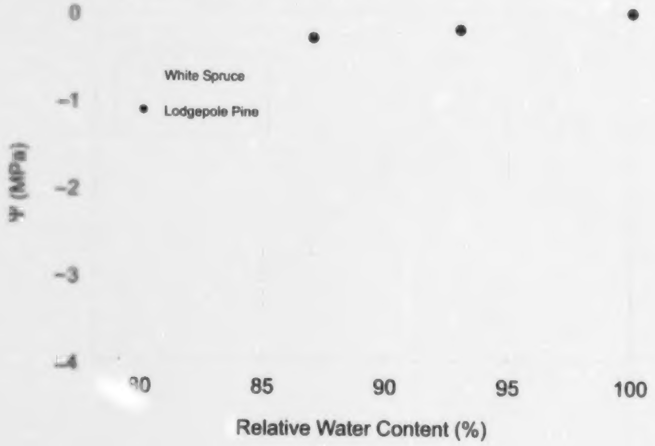
Fig. 2.1.1*b*. Seasonal change in osmotic potential at saturation (Ψ_{sat}), also called full turgor, and turgor loss point (Ψ_{tlp}), or zero turgor, and relative water content turgor loss point (RWC_{tlp}) for interior spruce seedlings shoot systems (mean ± SE). Shoot phenological stages are defined by (BB) budbreak, (SE) shoot elongation, and (BI) bud initiation (adapted from Grossnickle et al. 1996*a*).



Another component of drought tolerance is cell wall elasticity. High cell wall elasticity, or the improved ability of tissue to shrink or expand, allows turgor pressure to be maintained at lower tissue relative water contents, thereby preventing mechanical damage to cell membranes under moderate to severe drought. Conversely, tissues having low cell wall elasticity quickly develop a low Ψ and thereby maintain a gradient for water uptake along the soil–plant–atmosphere continuum (Section 2.1.2) from drying soils without undergoing large tissue water deficits. A low level of cell wall elasticity also reflects greater resistance to deformation of the cell walls and, therefore, a greater ability of the cells to retain water as plant Ψ decreases. This preserves high tissue relative water contents while turgor pressure decreases, thereby providing tolerance against lethal drought. Spruce species are reported to have a low level of cell wall elasticity (i.e., a high relative water content at turgor loss point) during the growing season (Colombo 1987; Grossnickle 1988*b*, 1989; Zine El Abdine et al. 1994*a*) (Fig. 2.1.1*b*). A species that has low cell wall elasticity can have a rapid loss in physiological activity, with a small decrease in cell water content (Abrams 1988).

Spruce species primarily uses changes in Ψ_π rather than cell wall elasticity to maintain drought tolerance. This is represented by the minor change in the relative water content turgor loss point throughout the entire year (Fig. 2.1.1*b*). Spruce is a genus that generally has a turgor loss point at high relative water contents (i.e., 84–90%). This is typical of species that live in moist habitats (reviewed by Bannister 1976). When white spruce was exposed to a water deficit, their inherently low cell wall elasticity caused a rapid development of low Ψ in comparison to pine species (Fig. 2.1.1*c*). This contrast occurs because pine species have tissues with highly elastic properties that can undergo greater changes in cell volume, maintain higher Ψ_P, and have higher physiological activity, as

Fig. 2.1.1c. Xylem water potential (Ψ) (mean ± SE) at various relative water contents for white spruce and lodgepole pine (*Pinus contorta* Dougl.) during early spring (adapted from Cowling and Kedrowski 1980).

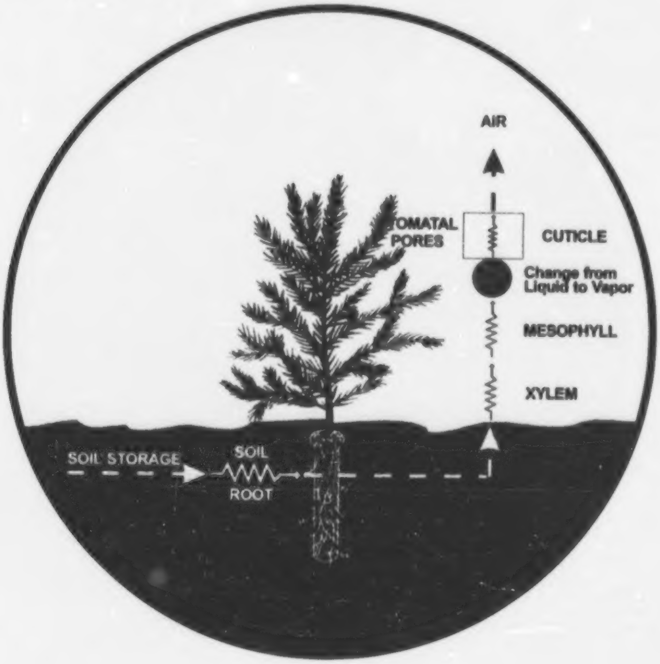


water content decreases (Grossnickle 1988*b*). Spruce species, compared to pine species, use more of a drought avoidance strategy (i.e., reduces physiological activity to preserve high tissue relative water contents) (Jarvis and Jarvis 1963*b*; Grossnickle and Blake 1987*a*; Grossnickle 1988*b*) to withstand a water deficit.

2.1.2 Water movement through the plant

Water moves along a pathway from the soil through the plant and then into the air through the soil–plant–air continuum, SPAC. The driving force for this water movement along the SPAC is the Ψ gradient between soil, plant, and the atmosphere, which is driven by the vapor pressure gradient between needles and the air. Any combination of increasing air temperature or decreasing relative humidity can increase VPD (Section 1.3.2). Also, as the relative humidity of the air decreases below 100%, its affinity for water increases dramatically, thereby causing a very rapid drop in the Ψ (Section 1.3.2). The resulting effect of this very steep Ψ gradient from the plant to the air is to lower the needle Ψ, which starts the process of water moving from a location of higher Ψ (i.e., the soil) through the plant into the air (Fig. 2.1.2*a*). The concept of the SPAC is useful in illustrating how water moves through the soil, roots, stems, needles, and evaporates into the air, and the driving forces and resistance operating at each stage.

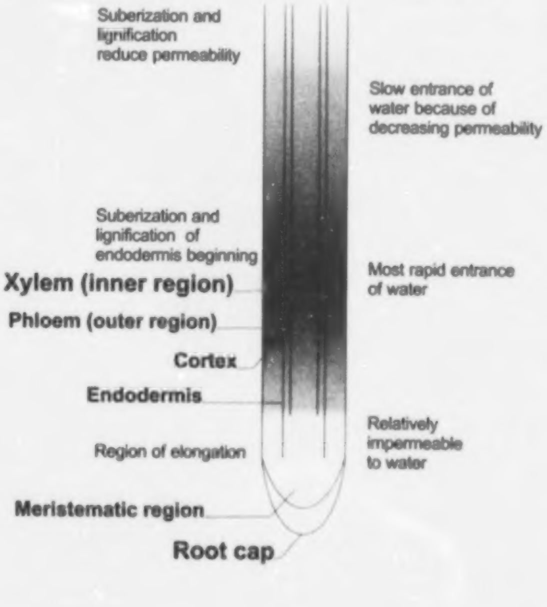
Fig. 2.1.2*a*. A simplified diagram showing water flow through the soil–plant–air continuum (SPAC) for a spruce seedling. Points identified by the jagged lines indicate locations of resistance to water and vapor flow.



Water moved through a seedling during the daily transpirational process is primarily stored in the soil (Fig. 2.1.2*a*). The amount of soil water that is available to the seedling is dictated largely by soil texture and water content (Section 1.3.1). The soil texture determines the degree of attractive capillary forces between the soil particles and water in the soil (i.e., soil matric potential), which, along with soil Ψ_π, constitutes the soil Ψ. This soil Ψ must be overcome by the roots of plants (i.e., a lower root Ψ) in order to move water through the soil to the root surface.

Water moves through the soil and plant in a liquid form. Water moving through the SPAC encounters resistance to flow in the soil at the soil–root interface (Fig. 2.1.2*a*). Resistance at the root surface is one of the major impediments to water flow along the SPAC of Sitka spruce trees (Hellkvist et al. 1974) and conifer seedlings (Running and Reid 1980). Water and solutes move along the Ψ gradient by diffusion from cell to cell (i.e., either across vacuoles or through cell walls) through the parenchyma of the root cortex until it reaches the endodermis (Larcher 1995) (Fig. 2.1.2*b*). In the root endodermis, all inflowing water is channeled to particular sites through which it can pass. This diffusionary process of water movement through the roots restricts water flow if edaphic conditions (e.g., low soil temperatures, Section 3.5.1; flooding, Section 3.5.2.2) limit physiological processes. Root resistance to water uptake is variable, depending upon the amount of new root development. New unsuberized spruce roots allow for a more efficient uptake of water (i.e., lower resistance to water flow or higher hydraulic conductivity) than suberized roots (Grossnickle 1988*a*; Häussling et al.

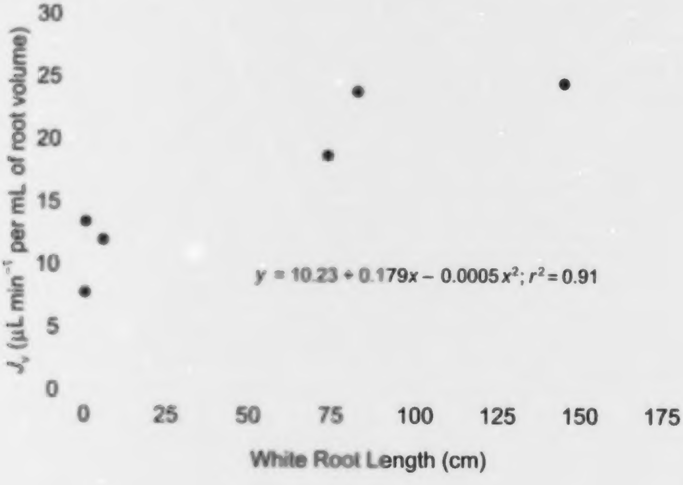
Fig. 2.1.2*b*. Diagrammatic representation of a root from a spruce seedling, showing the relationship between anatomy and absorbing regions for water.


Suberization and lignification reduce permeability
Slow entrance of water because of decreasing permeability
Suberization and lignification of endodermis beginning
Xylem (inner region)
Most rapid entrance of water
Phloem (outer region)
Cortex
Endodermis
Relatively impermeable to water
Region of elongation
Meristematic region
Root cap

1988; Rüdinger et al. 1994). That is because the root region that has just completed elongation allows the most rapid movement of water to the xylem (Fig. 2.1.2*b*). For example, root hydraulic conductivity increased in black spruce seedlings with greater new root length (Fig. 2.1.2*c*). This ability of newly developed roots to have high water uptake capability is important because it allows seedlings to maintain a proper water balance throughout the daytime, thereby decreasing the chances of water stress that can occur in recently planted spruce seedlings (Section 5.3).

Water movement through the xylem occurs under a negative Ψ (usually between –1 and –2 MPa) and usually encounters relatively low resistance. Water is conducted through the xylem pathway which has developed to allow for the long-distance transport of water (Fig. 2.1.2*a*). Water movement in conifers occurs through a xylem system made up of a series of tracheids, while angiosperms and herbaceous species have a xylem system consisting of vessels. In conifers, water must pass through a xylem system made up of thousands of tracheids, each tracheid being a single cell that is ~5 mm in length and up to 45 μm in diameter (Zimmerman 1983). As a result, there is considerably greater resistance to water movement through the tracheids of conifers compared to species having vessel-like xylem structures. Resistance through the xylem pathway of spruce species is much greater than reported for herbaceous species (Hellkvist et al. 1974) or hardwood tree species (Zimmerman and Brown 1971); resistance to water flow through spruce species is up to 25 times that of species having ring-porus or diffuse-porus xylem vessels. Although conifers have higher resistance to water movement through xylem, it is felt that SPAC water movement is not limited by

Fig. 2.1.2*c*. Relationship between white root length and maximum water flux (J_v) through the root system of black spruce seedlings (adapted from Colombo and Asselstine 1989).



resistance in the xylem, but rather is primarily due to resistances encountered as water crosses the living cells in the roots and leaves (Kramer and Kozlowski 1979).

Water must remain in a liquid phase for water flow within the xylem to continue. If a plant is exposed to severe enough water stress, cavitation of xylem elements can occur. Cavitation is caused by a break in the xylem water column, with xylem conduits filling with air (Tyree and Sperry 1989). A xylem conduit in this air-filled state is embolized and is not available to conduct water, thus leading to an increase in resistance to water movement through the xylem. The built-in redundancy of the xylem pathway insures that water conduction continues, although embolized xylem elements cause a reduction in overall xylem hydraulic conductivity (i.e., increased xylem resistance). Embolized xylem elements can be repaired, but only under rare occasions of positive xylem pressures. Otherwise, the development of new xylem elements during the next growing season are required to restore full hydraulic capacity of the xylem conducting system.

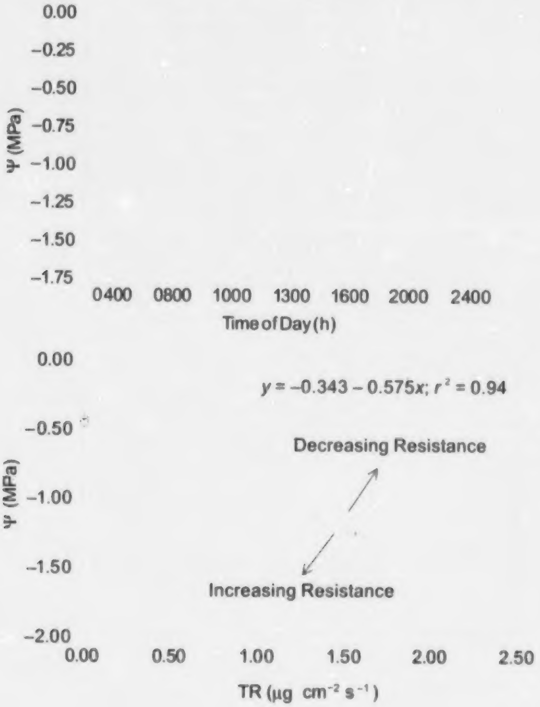
Water moves out of a plant as water vapor. Water evaporates from leaf tissue, or mesophyll, diffuses through the intercellular spaces in the leaf, and is lost through the stomata into the air (Figs. 2.1.2*a*, 2.2.1*a*). The rate of plant water loss, or transpiration, increases with decreases in relative humidity and rising temperature. This happens because of the very steep Ψ gradient from the plant to the air that occurs as relative humidity decreases (Section 1.3.2). The rate of water loss is proportional to the vapor pressure difference between the evaporating surface and the surrounding air and inversely proportional to any resistance that may be encountered, such as cuticular or stomatal resistance (Hinckley et al. 1978). Stomatal or cuticular resistance act to prevent excess water loss from the plant. Stomata, then, play a critical role in regulating water flow and maintaining a Ψ in a seedling that does not limit physiological processes (Section 2.2.1). From the needle surface, water vapor diffuses through the boundary air layer (i.e., a thin layer of still air surrounding the needle) and then into the turbulent air. Boundary layer thickness is a function of wind speed, leaf morphology, shoot structure, and orientation to the wind. Resistance of the boundary layer can reduce water loss from needles. Steepness of the vapor pressure gradient through the boundary layer is a critical factor affecting water vapor diffusion from the leaf to the air. The boundary layer resistance for spruce needles is relatively small because thin leaves have very low resistance to the diffusion of water vapor away from the leaf surface (Nobel 1991). For example, the boundary layer conductances (i.e., the reciprocal of resistance) for water vapor from Sitka spruce shoots are 0.07 and 0.1 m s^{-1} (i.e., resistances of 14.3 and 10 s m^{-1}, respectively) at wind speeds of 0.4 and 1 m s^{-1}, respectively (Whitehead and Jarvis 1981). Whitehead and Jarvis (1981) concluded that the rate of transpiration from conifer foliage was largely independent of boundary layer conductance.

As plant stomata open in the early morning and transpiration occurs, water starts to move through the SPAC from a source of higher Ψ (i.e., the soil) to a lower Ψ, under the pull of atmospheric evaporative demand (Fig. 2.1.2*a*). This pattern of water flow through the SPAC system is analogous to the flow of electricity in a conducting system and can therefore be described by the Ohm's law analogy (Hinckley et al. 1978; Pallardy et al. 1995) where

Water flow = difference in Ψ / resistance to water and vapor flow

As water flows along this pathway, any condition limiting water flow (i.e., higher resistance) along the SPAC decreases the Ψ in plants. A result of this resistance to water movement through the SPAC is that plant Ψ normally changes throughout the day in a diurnal fashion (Fig. 2.1.2*d*). Typically, established spruce seedlings have a Ψ that reaches a daytime low between –0.75 and –2.00 MPa, depending upon field site environmental conditions (Section 5.4.1.1). It is typical for spruce seedlings to be exposed to a daytime Ψ that can cause water deficits that limit some physiological processes (Section 2.1.3), but not at a level considered to cause damage. However, in certain instances

Fig. 2.1.2*d*. The diurnal change in Engelmann spruce seedling Ψ (mean ± SE) in relation to both the daily changes in evaporative demand of the air and the ability of the seedling to take up water from the soil system (adapted from Grossnickle and Reid 1984*b*). Also shown is the relationship between xylem water potential (Ψ) and transpiration rate (TR) for Engelmann spruce seedlings as seedling Ψ changes over the day. In this example, Ψ is the energy required for the flow of water (represented by TR; TR per unit needle area = stomatal conductance per unit needle area × VPD), with the slope of the relationship between these two parameters being the resistance to water flow along the SPAC. If the slope becomes more negative, resistance to water flow increases (i.e., greater changes in Ψ at similar rates of TR). If the slope becomes less negative, resistance to water flow decreases.

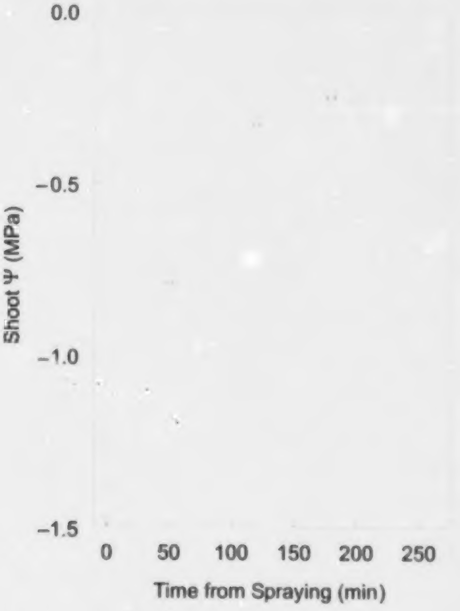


spruce seedlings can reach very low midday minimum Ψ when they are exposed to low soil water (Section 3.5.2.1) or to the phenomenon of planting stress (Section 5.3).

At night, water continues to move through the SPAC from a source of higher Ψ (i.e., the soil) to a lower Ψ in the shoot system of seedlings. Since stomata are usually closed, water uptake during the night eventually is sufficient for the seedling and the soil to reach comparable values of Ψ. This is why the measurement of seedling Ψ just prior to sunrise (Fig. 2.1.2*d*) (i.e., predawn shoot water, Ψ_{pd}) is reflective of a plant's equilibration to the root zone soil water potential and determines the water status with which a plant begins a daylight period (Ritchie and Hinckley 1975).

Water can also be absorbed through the shoots of spruce species. The permeability of needles to water and nutrients is high when shoots are expanding and declines with further development of the shoot system (Orem and Sheriff 1995). In mature Norway spruce shoot systems, water absorption through the needles is minimal, with absorption occurring primarily along the pathway of rays and parenchyma cells from the bark and wood to the xylem (Katz et al. 1989). The low absorption of water through the needles is due to the development of the cuticle around the needles as an effective barrier for reducing water loss (Section 2.2.1). As a result, shoot Ψ increases when the shoot surface is sprayed with water (Fig. 2.1.2*e*). This occurs due to the mass flow of water into a shoot system,

Fig. 2.1.2*e*. Increase in xylem water potential (Ψ) of Norway spruce shoots in relation to the time from initial spraying of the shoots with water (adapted from Katz et al. 1989).



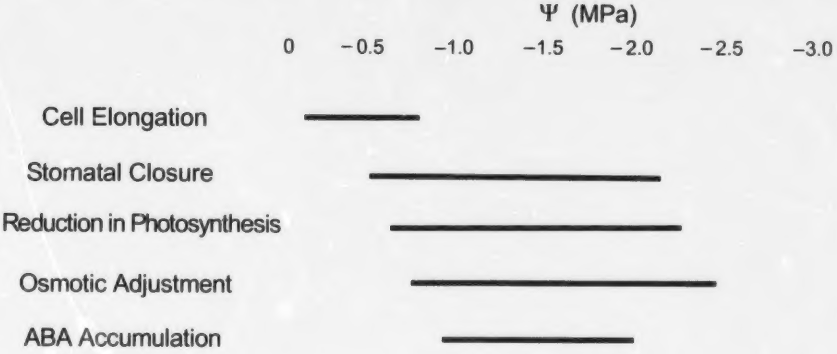
which is dependent upon the Ψ gradient between the shoot surface and the Ψ within the shoot system. In other words, for a fixed resistance, greater water uptake occurs when there is a steep Ψ gradient. Absorption of water through the shoot system is not important to the water budget of spruce seedlings under mesic conditions. This phenomenon of water absorption through the shoot system may be important in creating a favorable seedling water status during the growing season, when there is a dry soil, whereby recovery of seedling hydration can occur under conditions of heavy fog, dew (Section 1.3.2), or light rain. Water absorption through the shoot system may also be important in creating a favorable seedling water status during the winter, when the shoots are exposed to winter desiccation (Section 3.7.5).

2.1.3 Response to changing water potential

Plants respond to changes in Ψ with a combination of mechanistically linked responses and characteristics that comprise a particular type of behavior. Water stress occurs in trees "...when a decrease in water content, or an increase in water deficit, reaches a level which negatively affects a physiological process..." (Teskey and Hinckley 1986). Each plant species avoids or tolerates water stress through a combination of physiological responses (Jones et al. 1981; Kramer and Boyer 1995; Ludlow 1989). These responses are categorized as drought avoidance, drought tolerance, and drought resistance. Drought avoidance is the postponement of dehydration by plants. It is primarily determined by the reduction of water loss from the needles (i.e., cuticular development and stomatal control), a very efficient water transport system (i.e., conducting capability of the xylem), or through the maintenance of water uptake (i.e., increased rooting). Drought tolerance is the capacity of the protoplasm of a plant to undergo dehydration without irreversible injury and is primarily determined by the maintenance of turgor (i.e., tissue elasticity and solute accumulation) or through desiccation tolerance (i.e., protoplasmic and chloroplast tolerance to drought). Drought resistance is defined as the combination of drought avoidance and tolerance mechanisms. Each species uses these response mechanisms in different ways in an attempt to maintain physiological activity under changing Ψ.

Different physiological activities in a plant cease to function at different values of Ψ (Fig. 2.1.3). The range of Ψ values depicted in Fig. 2.1.3 is meant to provide a generalization of changes in physiological responses that can occur in spruce species throughout the growing season. The exact Ψ that causes a change in a physiological response is related to the plant's phenological state (Section 3.9). Typical daily changes in the Ψ of plants have varying degrees of influence on their performance. Thus, low Ψ should not always be considered as having a detrimental effect on plant performance. In fact, low values of Ψ in plants are important for nutrient uptake because this deficit creates the Ψ gradient that is needed for the movement of ions through the soil to the roots (Sections 2.3.1 and

Fig. 2.1.3. Generalization of changes in morphological development and physiological responses of spruce species as they are exposed to a range of water potential (Ψ) values (compiled from Sections 2 to 4).



3.6.1). Plants regularly undergo a range of Ψ values on any given day (Fig. 2.1.2*d*). Certain plant processes cease functioning while the plant is exposed to a specific Ψ. Spruce species are considered to be under water stress when they are exposed to these lower values of Ψ. When the plant is recharged from water in the soil, the low Ψ is relieved and these physiological activities resume. Conifer seedlings start to die when shoot Ψ exceeds –4.0 to –5.0 MPa (McDonald and Running 1979). This indicates that spruce seedlings can withstand very low Ψ before water stress causes death.

2.2 Gas exchange

Gas exchange, as a general term, can be defined as the movement of water (H_2O) vapor and oxygen (O_2) out of plants and the movement of carbon dioxide (CO_2) and O_2 into plants by diffusion through needle stomata. During photosynthesis, plants take up CO_2 and give off O_2, whereas in respiratory gas exchange the direction of these two gases is reversed. Gas exchange results from the presence of a gradient between the internal needle surface and surrounding air; during the daytime, when photosynthesis is occurring, CO_2 diffuses into the needles by way of open stomata while H_2O vapor diffuses out into the drier surrounding air.

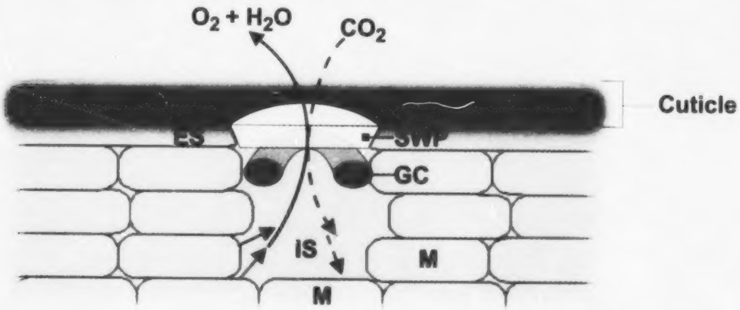
Gas exchange encompasses three different processes critical to the physiological functioning of a plant. These include the following: (*i*) transpiration, (*ii*) photosynthesis, and (*iii*) respiration. A brief overview of stomata and stomatal function is presented, and then each of the above gas exchange processes are defined and discussed. Readers interested in in-depth information on gas exchange processes in plants should reference Salisbury and Ross (1992).

2.2.1 Stomata and stomatal conductance

Stomata are pores that exist on the surface of plant leaves, or needles in the case of conifers. The pore, or actual opening of the stomata, is called the aperture. Stomatal pores on spruce needles are located within an indentation in the needle epidermis (Fig. 2.2.1*a*). There is a distinct antechamber above the pore that is shaped like a cup or inverted cone; it is approximately 13–18 µm in depth (Jeffree et al. 1971; Vanhinsberg and Colombo 1990). This antechamber is filled with a porous wax plug that consists of intermeshed tubes of wax (Jeffree et al. 1971). Gases such as O_2, H_2O, and CO_2 are able to diffuse through this wax plug, but its presence reduces the area within the antechamber in which gases may diffuse and increases the diffusive resistance of gases. Each stomatal pore is surrounded by two specialized guard cells. Guard cells regulate the opening and closing of the stomatal pore. The stomatal pore opens into an intercellular space within the needle that is surrounded by mesophyll tissue. When stomata are open, O_2 and H_2O diffuse out of this mesophyll tissue into the intercellular space, through the stomatal pore, into the antechamber, and then into the atmosphere. CO_2 follows this same pathway into the needle when stomata are open. Due to the geometrical nature of the stomatal structure in Sitka spruce, the resistance to the flow of CO_2 into the needles and H_2O out of the needles can be attributed, in equal portions, to the wax plug in the antechamber, the stomatal pore, and intercellular spaces within the needles (Jeffree et al. 1971). This tortuous pathway restricts the free flow of gasses and is the method by which spruce species regulate the flow of O_2 and H_2O out of, and CO_2 into, the needles.

The remainder of the spruce needle is covered with an epidermal layer. The distinguishing characteristic of the needle epidermis is the presence of cutin, a fatty waxlike substance, in the cell walls. Cutin is most notable on the external needle surface, where it creates a cuticular layer of epicuticular waxes (Esau 1965). These epicuticular waxes constitute 1–1.5% of the needle dry weight of

Fig. 2.2.1*a*. Diagrammatic representation of a stomatal pore on a spruce needle and the directional flow of gases during the photosynthetic process. The following terms define the abbreviations: ES, epidermal surface; SWP, semi-permeable wax plug; GC, guard cells; IS, intercellular space; M, mesophyll tissue.

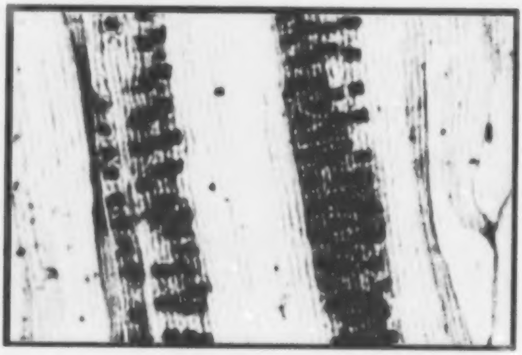


newly developed needles on black, Norway, red, and white spruce seedlings (Cape and Percy 1993). This cuticle layer extends over the entire needle surface and down into the stomatal antechamber (Fig. 2.2.1*a*). The cuticle protects the needles from excessive water loss, thereby restricting most water loss through the stomata on the needles. Complete cuticular development on spruce needles takes a minimum of 3 months from the time of budburst in spruce species (Tranquillini 1979). The final thickness of the cuticle is not usually reached until sometime during early fall (Tranquillini 1976). Cuticular development is reduced under shorter growing seasons, with low air temperatures considered a dominant factor (Tranquillini 1976; Vanhinsberg and Colombo 1990). Once the cuticle is fully developed, it can range from ~0.4 to 1.5 μm in thickness for trees growing in the field, with 2-year-old needles having greater thickness (Baig and Tranquillini 1976). Spruce seedlings grown in a greenhouse environment have a fully developed cuticle of up to 3.35 μm in thickness (Vanhinsberg and Colombo 1990). Complete cuticular development is important because Norway spruce needles with a fully developed cuticle have a rate of cuticular transpiration that is only ~5% of a needle with a poorly developed cuticle (<0.4 μm in thickness) (Baig and Tranquillini 1976). Spruce needles with fully developed cuticles and closed stomata transpire at only 2–3% of the rate of needles with open stomata (Beadle et al. 1979; Larcher 1995). The diffusion of water through the cuticle involves water dissolution in the lipophilic medium of the cuticle at the cell wall – cuticle interface, diffusion through the solid matrix, and finally desorption from the outer surfaces of the cuticle membrane (Kerstiens 1996). Cuticular conductance also declines in spruce needles under drought stress (Beadle et al. 1979). When fully developed, the cuticle provides spruce species with an effective drought avoidance mechanism for preventing water loss through the needles.

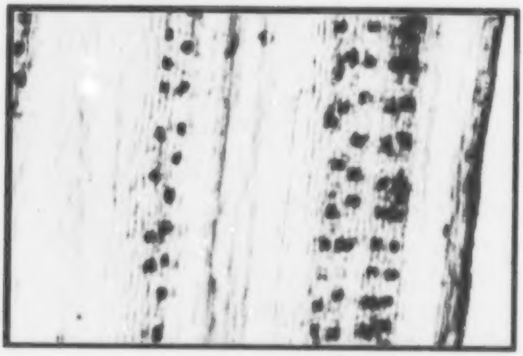
Stomatal size and density vary widely among species. Usually species with few stomata per unit of leaf surface area tend to have large stomata, while those with many stomata have smaller stomata. In general, conifers have stomatal pores that range from 15 to 20 μm in length and stomatal density from 20 to 120 cm^{-2}, which comprise approximately only 0.3–1.0% of the needle surface area (Larcher 1995). Stomata are found in rows that run lengthwise along a spruce needle and are found along all four sides of the needle (Fig. 2.2.1*b*). The number of stomata within a row and the number of rows of stomata on spruce needles vary, depending upon the genetic source. This example shows how the number of stomata within a row and the number of rows of stomata decrease as one moves from Sitka spruce to interior spruce genetic sources. These stomatal density patterns have a direct effect on gas exchange processes (Section 4.1).

Stomatal conductance (g_{wv}) describes the relationship between stomatal aperture and the diffusion of water vapor; g_{wv} is directly proportional to the width of the stomatal pore. The size of the aperture is controlled by turgor of the guard cells. Aperture size increases with increased turgor and decreases with decreased turgor. Diffusion of gases through the stomata increases in direct proportion to increasing pore width. The total stomatal aperture area of a needle is determined

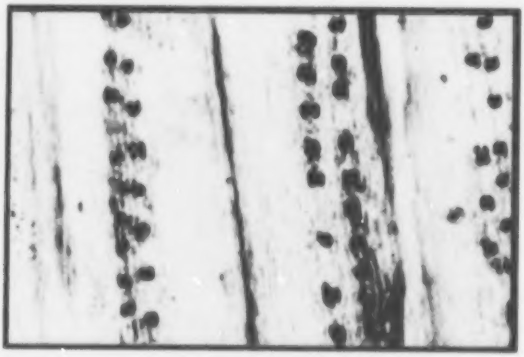
Fig. 2.2.1*b*. Photograph of stomata on a Sitka spruce, Sitka × interior spruce hybrid, and interior spruce needles (× 200). Guard cells are located on either side of the stomatal pore (photographs provided by S. Fan).



Sitka Spruce



Sitka x Interior Spruce Hybrid



Interior Spruce

by a combination of the number of stomata per area of needle surface and the maximum width of each stomatal pore. In general, the opening capacity of stomata for conifer species is low compared to herbaceous species, which is why conifer species have lower rates of maximum g_{wv} compared to herbaceous species (Körner et al. 1979).

Stomata open and close, depending upon the environment surrounding the plant, and in essence, regulate the plant's response to its environment where gas exchange is concerned. Sections 3.1–3.5 discuss stomatal response of spruce to environmental factors. Thus, g_{wv} acts as an indicator of how a plant responds to site environmental conditions.

Stomata along a spruce needle may not always respond uniformly to site environmental conditions. Norway spruce needles can have a patchy distribution of stomatal responses to stress effects (Beyschlag et al. 1994). In other words, some stomata remain open while other stomata partially close or completely close in response to stress. If environmental stress becomes severe enough, all stomata close. The advantage of patchy stomatal closure in response to environmental stress is unclear. Further work is required to define the relevance of this phenomenon to the gas exchange process of spruce needles.

2.2.2 Transpiration

Transpiration can be simply defined as water vapor loss from leaves. It is both a physical and physiological process. The physical process deals with evaporation, which is a function of both the needle temperature and vapor pressure deficit of the air. Transpiration occurs because of the large Ψ gradient that exists between the water on the surfaces and within the leaf, and the surrounding air (Section 1.3.2). In essence, water vapor diffuses from the leaf tissue via the open stomata. Even in humid atmospheric conditions, there is a significant Ψ gradient and transpiration occurs. This physiological process is affected by regulating factors of the plant such as leaf structure and stomatal behavior.

Transpiration usually occurs in two stages. First, water evaporates from cell walls into the intercellular spaces within the needle tissue. Second, water vapor diffuses from the intercellular spaces through the stomata and out into the air surrounding the needles (Fig. 2.2.1*a*). Transpiration is an important factor in plant water relations. The evaporation or loss of water from the leaf tissue creates the Ψ gradient that causes movement of water through plants (Section 2.1.2).

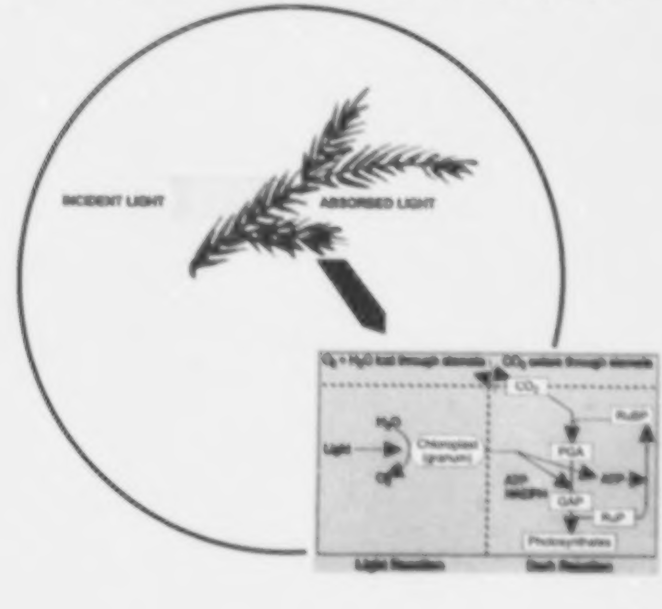
2.2.3 Photosynthesis

Photosynthesis is the process by which light energy is converted into the chemical energy necessary for plant growth and development. It is driven by three major processes: the photochemical process, the enzymatic process requiring no light, and the process of diffusion of gases between the chloroplasts and the outside air. Each of these major processes are influenced by internal and external factors that can limit the yield of chemical energy derived from the overall photosynthetic process. The following section briefly describes the three major processes of photosynthesis.

The photochemical process is a light reaction. Leaves absorb more than 90% of the violet and blue wavelengths and almost a comparably high percentage of orange and red wavelengths, while absorbing very little of the green wavelengths (Salisbury and Ross 1992). Interestingly, the epidermal–hypodermal layers, which give spruce needles their rigidity, also alter light penetration. These epidermal–hypodermal layers can attenuate 20–40% of the incident radiation on an Engelmann spruce needle (Stenberg et al. 1995). This indicates that a substantial amount of light is lost as light penetrates a spruce needle to reach the light reaction centers of the photochemical process. In the photochemical process, light is captured by chloroplasts, which are the chlorophyll-containing bodies in leaf tissue cells. Not all of the absorbed light energy is involved in photosynthesis. Of the light that is absorbed by chloroplasts, less than 5% is involved in photochemical reactions (Section 1.1). After light is captured, the photochemical process is initiated (Fig. 2.2.3*a*). This process generates NADPH (reduced nicotinamide adenine dinucleotide phosphate) and energy in the form of ATP (adenosine triphosphate) for the enzymatic stage of photosynthesis.

The energy, or reducing power, gained in the photochemical process is used to reduce or change CO_2 into different photosynthates, which in turn can be converted to carboxylic acids and amino acids in subsequent chemical reactions.

Fig. 2.2.3*a*. Simplified scheme to show the photosynthetic process found in the chloroplasts of C_3 plants (e.g., spruce needles). Definition for abbreviations of terms is as follows: RuBP, ribulose-1,5-biphosphate; PGA, 3-phosphoglyceric acid; ATP, adenosine triphosphate; NADPH, reduced nicotinamide adenine dinucleotide phosphate; GAP, glyceraldehyde-3-phosphate; RuP, ribulose-5-phosphate.



This enzymatic stage of photosynthesis is sometimes referred to as the dark reaction (Fig. 2.2.3*a*). This stage occurs in the chloroplasts, specifically in the stroma of the chloroplasts. In C_3 plants (e.g., spruce species), this process is initiated when CO_2 bonds to ribulose-1,5-biphosphate (RuBP). This RuBP then undergoes carboxylation which is catalyzed by the enzyme ribulose biphosphate carboxylase–oxygenase (Rubisco). Each RuBP molecule is hydrolized into two 3-phosphoglyceric acid (PGA) molecules. Each of these PGA molecules contains three carbon atoms, which are the first stable products of photosynthesis, giving rise to the name C_3 pathway. The reducing power of NADPH and energy stored in ATP reduces PGA into glyceraldehyde-3-phosphate (GAP). Some of the GAP molecules then flow into a pool of various carbon compounds, which provides the material for photosynthates. Other GAP molecules are converted into ribulose monophosphate (RuP; ribulose-5-phosphate) which is then phosphorylated by ATP to form RuBP which can then accept CO_2 to continue the cycle. The rate of this enzymatic process is highly dependent on CO_2 supply, temperature, cell water potential, nutrient availability, and the developmental stage of the plant; indicating that optimum microclimatic conditions are critical in order for plants to produce the photosynthates required for growth.

The process of diffusion brings about the entry of CO_2 through open stomatal pores to chloroplasts from the air (Fig. 2.2.1*a*). This process links photosynthesis to external air temperature and relative humidity. As stomata open, CO_2 enters intercellular spaces within the leaf, is absorbed through the mesophyll cell walls, becomes dissolved in water, and migrates to chloroplasts where it is reduced into photosynthates during the enzymatic process (Fig. 2.2.3*a*). Environmental factors influencing stomatal opening affect photosynthesis in spruce species (Section 3).

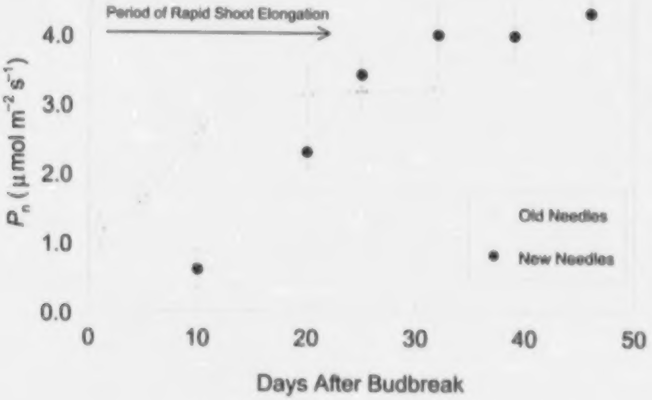
Photosynthesis, then, is a process in which light and CO_2 enter the plant and are converted into the chemical energy, or photosynthates, needed for plant growth and development (Fig. 2.2.3*a*). The term net photosynthesis (P_n) is often used in ecophysiological response studies and is defined as the difference between gross photosynthesis (i.e., total CO_2 fixed by a plant) and the CO_2 used in respiration. The term P_n is used to describe the photosynthetic response of spruces species throughout this treatise.

Photosynthates are the primary product of the photosynthetic process. These photosynthates (i.e., sugars, starch, carboxylic acids, amino acids) are the energy storage compounds and the basic organic substances from which most other organic compounds found in plants are synthesized. Most photosynthates are translocated via the phloem, which is the vascular pathway that transports photosynthates and redistributes nutrients to various locations in the plant. An actively growing seedling is an integrated system, with all growing points competing for photosynthates. Thus, the direction of translocation and the amount of photosynthates moved to various locations in the seedling depend upon both the food requirements of various sinks and the magnitude of supply being produced by the photosynthetic process. Relative distance from the source of photosynthates is also important, with sinks usually being supplied from the nearest source. During the growing season, the relative strength of various sinks and thus the preferential translocation of photosynthates in a seedling are as follows: young needles and stem tips > mature needles > cambial region in the shoot stem > root system > storage (Kozlowski and Pallardy 1996). This preferential translocation of photosynthates is one reason why spruce species have seasonal shoot and root growth patterns that are offset; the primary periods of root growth occur prior to budbreak in the spring and after budset in the fall (Section 2.6.2).

Seedling growth is dependent on the photosynthates produced by photosynthesis. As a result, it seems logical that if the rate of P_n could be increased, growth would increase. However, poor correlations often exist between short-term measurements of P_n and growth (Kozlowski et al. 1991). This poor correlation is partly due to the fact that growth is related not only to instantaneous measurements of P_n, but also to leaf area, leaf age, leaf exposure to sunlight, seasonality of P_n, and P_n throughout the crowns. In addition, not all photosynthates are used for growth, with a portion also used for maintenance respiration. Evidence now indicates that, in conifers, growth limits P_n (Luxmoore 1991; Luxmoore et al. 1995). This theory is based on the following evidence. First, growth is more sensitive than photosynthesis to water stress (Section 2.1.2) and nutrient deficiency. Second, because the growth sinks are sensitive to these environmental limitations, reduced growth leads to a reduced demand for photosynthates. This reduced demand for photosynthates causes a reduced translocation of photosynthates from needles, resulting in a feedback regulation of P_n. These findings have lead to speculation that growth limits photosynthesis rather than photosynthesis limiting growth.

The photosynthetic activity of spruce needles varies, depending upon age. As buds break and needles emerge in the spring, the needles gradually develop photosynthetic capacity. During needle expansion, the photosynthetic rate is low and respiration is high, resulting in low P_n (Fig. 2.2.3*b*) (Ludlow and Jarvis 1971). As needles further develop in the spring, they quickly reach a high level of photosynthetic capacity that is comparable to 1-year-old needles. This rapid change in P_n is attributed to either the increase in the enzymatic activity related to the photosynthetic process as needles mature, or to the development of suitable sinks for the photosynthetic products (Ludlow and Jarvis 1971). Spruce needles are able to maintain a high level of photosynthetic capacity for up to 4 years (Hom and Oechel 1983; Sullivan et al. 1997), but the photosynthetic capacity begins to decline as the needles age over a number of years (Ludlow and Jarvis 1971). Hom and Oechel (1983) attributed the ability of black spruce needles to maintain a high photosynthetic capacity, for up to 4 years, to high nitrogen and phosphorus levels. The P_n in spruce species is related to nitrogen and phosphorous content, with high P_n occurring at greater needle nutrient content (Section 3.6.2). The decline in P_n as spruce needles age is attributed to increased stomatal and mesophyll resistance, reduced stomatal activity, the accumulation of wax in

Fig. 2.2.3*b*. Change in net photosynthesis (P_n) of newly developing and older interior spruces needles ($N = 10$: mean ± SE) during the period just after budbreak in spring (S. Fan and S. Grossnickle, unreported data).



the stomatal cavities, and nonreversible winter chloroplast degradation (Ludlow and Jarvis 1971; Jeffree et al. 1971). The decline in photosynthetic performance for spruce needles occurs over a number of years, with needles up to 13 years of age still maintaining 40% of the photosynthetic capacity of newly developed needles (Hom and Oechel 1983). This ability of spruce species to maintain a positive carbon budget reduces maintenance respiration costs of retaining older needles and favors a positive overall carbon balance.

Water use efficiency (WUE) describes the relation between plant production (i.e., carbon fixed) and the amount of water that is lost during transpiration. Water use efficiency provides information on the ability of a plant to balance the process of accessing carbon, through photosynthesis, to allow growth to occur in relation to the loss of water. Within the context of gas exchange processes in plants, instantaneous WUE is defined as the amount of CO_2 taken up through the process of photosynthesis in relation to the amount of water lost through transpiration into the surrounding air. The concept of intrinsic WUE is also used, which is defined as the amount of CO_2 taken up through the process of photosynthesis in relation to stomatal opening measured through g_{wv}. Carbon isotope composition ($\delta^{13}C$) provides a long-term integral measure of plant and environmental parameters that influence gas exchange processes, thus WUE, over the time that carbon is fixed (Farquhar et al. 1989). The present day content of $^{12}CO_2$ and $^{13}CO_2$ in the atmosphere is approximately 98.9 and 1.1%, respectively. Short- or long-term WUE can be determined through measurements of the relative abundance of stable carbon isotopes ^{13}C and ^{12}C in plant organic tissue. This approach is based on discrimination against fixation of $^{13}CO_2$ by the photosynthetic process. This is due to primarily the fact that $^{13}CO_2$ diffuses more slowly from the air through stomatal pores to the sites of carbon fixation, and Rubisco preferentially fixes $^{12}CO_2$ in the dark reaction of photosynthesis. Thus, $\delta^{13}C$ of needles is a function of both the supply of CO_2 to sites of carbon fixation and the demand of the chloroplasts for CO_2 (i.e., photosynthetic capacity). As a result, the ratio of ^{13}C to ^{12}C in C_3 plants tends to be lower than found in the atmosphere. In general, C_3 terrestrial plants have $\delta^{13}C$ values that range from –23 to –36‰ (Larcher 1995). The reported values of $\delta^{13}C$ for spruce species range from approximately –26.0 to –31‰ (Flanagan and Johnsen 1995; Heaton and Crossley 1995; Sun et al. 1996; Grossnickle and Fan 1998; Livingston et al. 1999). This indicates that spruce species have fairly comparable $\delta^{13}C$ values and that these $\delta^{13}C$ values are comparable to other C_3 terrestrial plants. A detailed discussion of the $\delta^{13}C$ approach for measuring WUE in plants is presented elsewhere (Ehleringer et al. 1993). Long-term WUE is also determined by the ratio of dry matter produced to the amount of water used by the plant over the growing season. All of these approaches essentially describe the fact that in order for a plant to take up CO_2, it has to expend water, and when it reduces the amount of water lost, there is a reduction in the uptake of CO_2. Detailed discussion of WUE concepts can be found in a number of other sources (e.g., Kozlowski and Pallardy 1996; Lambers et al. 1998). A brief discussion of WUE for spruce species is presented at a number of points throughout this treatise.

2.2.4 Respiration

Respiration is the process in which photosynthates in living cells are used, or oxidized, resulting in the release of energy and CO_2. Respiration occurs continuously in all living cells, but is more pronounced, or rapid, in meristematic regions that have high rates of physiological activity or growth. Regions of high respiration include the cambium (inner bark layer), root and stem tips, and young shoot tissue. It has been estimated that between 30 and 70% of the total carbon fixed by plants is used in the respiration process (Sprugel et al. 1995), indicating that respiration is a major factor in plant usage of energy reserves.

Another form of respiration, photorespiration, is a by-product of the photosynthetic process of C_3 plants (e.g., spruce species) in which O_2 rather than CO_2 binds to Rubisco during photosynthesis, resulting in a reduction in the overall rate of photosynthesis. Under normal atmospheric conditions, C_3 plants can have up to a 20% reduction in their photosynthetic process due to photorespiration (Larcher 1995). Larcher (1995) points out that photorespiration can have a beneficial effect by diverting excessive light energy, thereby protecting the photochemical process of photosynthesis. Photorespiration is not discussed any further; a detailed discussion is presented in Larcher (1995). Additional discussions on respiration pertain to dark respiration.

There are two purposes for respiration: construction and maintenance. Construction respiration is the generation of energy for the synthesis of plant dry matter, or more basically, growth. Annually, construction respiration accounts for 40–50% of total respiration in field-grown Norway spruce trees (Stockfors and Linder 1998). Maintenance respiration utilizes energy for maintenance of cell integrity, or health. For Engelmann spruce forests, maintenance respiration can account for 30–60% of total respiration during the growing season (Ryan 1990). It accomplishes such processes as protein turnover, stability of ion and metabolic gradients, and physiological adaptation to changing environmental conditions. The two respiration processes, construction and maintenance, produce different end products for different purposes. Both, however, use the same photosynthate supply, indicating that a greater need for maintenance respiration affects the amount of photosynthate available for construction respiration.

Respiration rates are affected by seasonal variation, specifically by the combination of temperature and physiological activity associated with growth. In the boreal forest, stem respiration rates for spruce reach a peak during the growing season and then decline when the trees are dormant (Section 3.3.3). Temperature, however, is the primary environmental variable affecting respiration. Maintenance respiration rates approximately double with each 10°C increase in temperature. The effect of temperature on maintenance respiration is quantified by the symbol Q_{10}. This refers to the ratio of respiration rate at temperature T to the rate of respiration at temperature $T - 10°C$. For a wide variety of plant species, the Q_{10} ranges from 1.6 to 3.0 (Amthor 1984). Thus, warm temperatures increase the use of photosynthates for maintenance respiration, decreasing the availability of these reserves for seedling growth. The effects of temperature on the respiration rates of spruce species are discussed in Section 3.3.3.

2.3 Plant nutrition

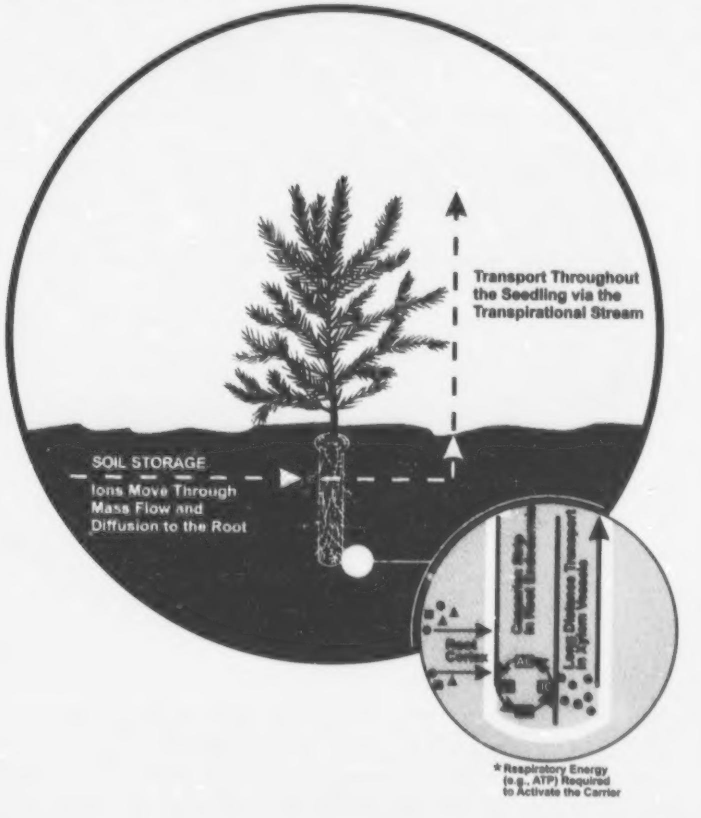
All green plants require the same basic set of mineral nutrients. These nutrients are used by all plants for essentially similar purposes. However, various species differ considerably in their nutrient requirements. An element is classed as an essential nutrient either if the plant cannot complete its life cycle without it or if it is part of a molecule of an essential plant constituent or metabolite (Epstein 1965). This section provides an overview of the following areas of plant nutrition as they relate to spruce species: (*i*) nutrient uptake, (*ii*) role of nutrients in plants, (*iii*) nutrient utilization and growth, and (*iv*) visible deficiency symptoms. Readers seeking further details on aspects of the basic physiology of plant nutrition should refer to Salisbury and Ross (1992), while readers should refer to Binkley (1986) for the importance of plant nutrition in forest ecosystems.

2.3.1 Nutrient uptake

Nutrients in the soil are supplied to the roots of a seedling, in part, through a passive uptake process. As roots grow out into the soil, they come in contact with exchangeable nutrients. Mineral ions come into and go out of solution as soil pH changes (Section 1.5.1). Conifer seedlings grow best at around pH 5.5 (Landis et al. 1989). Sitka spruce seedlings grew best at a pH of 4.5–5.0 (Leyton 1952), while Norway spruce seedlings grew best within a pH range of 4.75–6.60 (Brunner et al. 1999). This pH range allows for the availability of mineral ions in the soil solution at levels that are best suited for spruce seedling growth. In this soil solution, nutrients sometimes move towards the roots along a concentration gradient through the process of diffusion. In addition, as transpiration occurs and water flows through the SPAC (Section 2.1.2), there is a mass flow of ions as water moves to the roots (Fig. 2.3.1). The daily change in plant water potential that occurs due to transpiration of water from the needles creates a gradient along the SPAC. This water potential gradient is required for the mass flow of ions and water through the soil to the root surface.

When ions are taken up by roots, the resulting lower concentration gradient near the root surface causes a diffusion gradient with the surrounding soil so that ions move towards the root. When the demand for N and K ions exceeds delivery by mass flow, diffusion becomes the dominant mechanism for seedlings to access these macronutrients. In contrast, P ions are particularly immobile in most soils (Section 1.5.1). Seedling access to P is limited through mass flow and diffusion processes, and as roots grow out into the soil, they come in contact with anions of PO_4^{3-}, which are adsorbed to soil anion-exchange sites. The relative

Fig. 2.3.1. Diagrammatic representation of nutrient uptake from the soil and into a spruce seedling. The following terms define the abbreviations on the figure: AC, active ion carrier; IC, inactive ion carrier; ATP, adenosine triphosphate. Different geometric symbols represent specific nutrient ions.


Transport Throughout
the Seedling via the
Transpirational Stream
SOIL STORAGE
Ions Move Through
Mass Flow and
Diffusion to the Root
Root
Cortex
AC
IC
Long Distance Transport
in Xylem Vessels
* Respiratory Energy
(e.g., ATP) Required
to Activate the Carrier

mobility of nutrients in the soil solution and the rate of uptake by the spruce seedling determine whether mass flow, diffusion, or root growth, allowing for the contact with ions, predominates in the nutrient uptake process.

Once nutrient ions are adjacent to the roots, an active uptake process must occur to move these ions into the plant. Ions diffuse freely into the roots through the outer space of the root cortex as far as the endodermis (Fig. 2.3.1). Further penetration requires passage through the casparian strip, a band of waxy material concentrated on the radial wall of the endodermal cells. Plants possess uptake mechanisms capable of moving ions across the cell membranes of the casparian strip through an active uptake process. There is general agreement that the active uptake process is the dominant mechanism for nutrient uptake in plants (Salisbury and Ross 1992). This active uptake process is mediated by specific ion carriers present in root cell membranes. These carriers recognize specific nutrient ions and transport them to the internal vascular system of the root. Once across the membrane, the ion is released, the inactive carrier is regenerated, and it then diffuses back across the membrane to bind with another ion. As a result, nutrient ions accumulate in the roots across a considerable gradient. Active uptake increases if the soil solution has a high concentration of specific ions, although this process reaches a maximum rate if all carriers are saturated. In certain instances, there are competitive effects of ions having a similar charge (e.g., K^+ and NH_4^+) for uptake sites, indicating that these ions are competing for the same carriers. Virtually all ions are present in the root xylem solution in varying quantities, indicating that the ion barriers within roots are leaky. The active process of nutrient uptake within the root cell membranes requires energy that is derived from the photosynthetic process, making the process of nutrient uptake tied indirectly to environmental conditions, which affects P_n of a seedling. Nutrient uptake requires a suitable level of root metabolic activity, causing this process to also be tied to site edaphic conditions (e.g., soil water availability and soil temperature) which can limit the flow of ions to the roots and the ability of seedlings to actively take up ions from the soil solution (Section 3.6.1).

After passing through the root endodermis, ions enter the xylem. The xylem is the main pathway for nutrient transport from roots to the shoot (Fig. 2.3.1). Ions flow along with water in the transpirational stream to sites of use within the shoot system. Once nutrients are inside the seedling, they are internally cycled on a seasonal basis (Section 3.6.1). Current growth rate and nutrient uptake are the key variables that regulate nutrient translocation in conifers; these processes are independent of both internal reserves and external supply (Nambiar and Fife 1991). Thus, the internal movement of nutrients within a spruce seedling is the sum of net uptake of nutrients from the soil through the xylem sap, plus recirculation of nutrients via both xylem and phloem sap from areas of inactive to active growth. The concentration of ions within the xylem sap of Norway spruce trees changes with season (i.e., highest concentration in the spring during shoot elongation when soil water is high and soil temperature has increased), as well as with nutrient status of the site (Dambrine et al. 1995). As a result, the concentration of ions within the xylem sap is a reflection of availability of nutrients in the soil system, the ability of the root system to actively take up nutrients in relation to site edaphic conditions, and ongoing recirculation of nutrients within the seedling.

In spruce species, water (Section 2.1.2) and nutrients can also be absorbed through the shoots. Nitrogen can be absorbed by spruce shoot systems and translocated throughout the plant (Bowden et al. 1989; Lumme 1994; Macklon et al. 1996). The location of the uptake of nutrients through the shoots has been reported to be through the bark (Katz et al. 1989) and needles (Macklon et al. 1996). Over the course of a growing season, the amount of N entering spruce species can range from 1 to 10% of the total N that is required (Bowden et al. 1989; Lumme 1994; Macklon et al. 1996). This indicates that the uptake of nutrients, in this case N, through the shoot system is a minor component in spruce species acquisition of mineral nutrients.

2.3.2 Role of nutrients in plants

Plant nutrients are elements found in plants that are necessary for the normal functioning of the plant. The most abundant elements in plants are carbon (C), hydrogen (H), oxygen (O), and nitrogen (N). These elements make up about 95% of the plant dry weight. Other elements are found in concentrations between a few percent and a few parts per billion and are just as essential for normal plant functioning. Macronutrients are nutrients used by plants in relatively large amounts. These include N, calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), and sulfur (S). Micronutrients, nutrients used by plants in relatively small amounts, are iron (Fe), manganese (Mn), boron (B), copper (Cu), zinc (Zn), molybdenum (Mo), and chlorine (Cl). Further information on the importance of specific nutrients on plant performance are found in Salisbury and Ross (1992).

Nutrient elements in plants have three main functions (Bidwell 1979). First, nutrient elements are necessary components of biological molecules and structural polymers. Calcium, for instance, occurs in pectin, which forms the middle lamella of cell walls (Epstein 1972). Phosphorus not only plays a key role in the energy used in plant metabolism, such as ATP, but is also a constituent of phospholipids, including those of membranes (Epstein 1972). A second role of nutrients is electrochemical, e.g., balancing ionic concentration, stabilizing macromolecules and colloids, and neutralizing charges. Third, nutrients serve a catalytic function in enzymatic reactions. Zinc, for example, is a constituent or activator of several enzymes and regulates the level of auxin in plants, while Cu catalyzes protein synthesis (Bidwell 1979). Some macronutrients perform all three roles. Micronutrients are mainly involved in catalytic functions. Elements most closely associated with electron-transferring systems in plants are Fe, Cu, Cl, and Mo, which are able to function as electron mediators in nonenzymatic reactions. Primary metabolic roles for elements in conifer species are shown in Table 2.3.3.

2.3.3 Nutrient utilization and growth

Availability of nutrient ions affects seedling growth (Landis et al. 1989). If a seedling has a lower tissue concentration than required for normal physiological functioning, an element is deficient and limits growth (Fig. 2.3.3). Spruce seedlings usually exhibit visual symptoms of deficiency and a reduction in growth (Teng and Timmer 1996). At a slightly higher nutrient concentration, seedlings do not exhibit visual symptoms of nutrient deficiency, but have reduced growth (i.e., hidden hunger). When a nutrient is no longer limiting in a seedling, growth reaches an optimum level, and this is termed the optimum nutrient range, provided no other nutrient is limiting. Maximum spruce seedling growth occurs when all nutrients exceed these critical nutrient concentrations. The required shoot concentrations of each mineral nutrient for maximum growth of spruce seedlings are found in Table 2.3.3. Spruce seedlings exhibit maximum growth at fertility levels of N at 1.5–2.5%, P at 0.18–0.4%, and K at 0.4–1.95% (based on foliar analysis as a percent of dry matter). In Norway and Sitka spruce, the proportional balance of nutrient elements (by weight with N at 100%) at maximum growth for N, P, and K is 100, 16, and 55–50%, respectively (Ingestad 1979). Luxury consumption occurs when nutrients are available in greater amounts, but do not result in greater growth. If nutrient concentrations reach extremely high levels, nutrient toxicity can occur, causing a reduction in spruce seedling growth (Teng and Timmer 1996).

Fig. 2.3.3. Relationship between conifer seedling growth and nutrient concentrations. The critical point is the threshold tissue nutrient concentration where deficiency of a nutrient no longer limits growth (adapted from Landis et al. 1989).

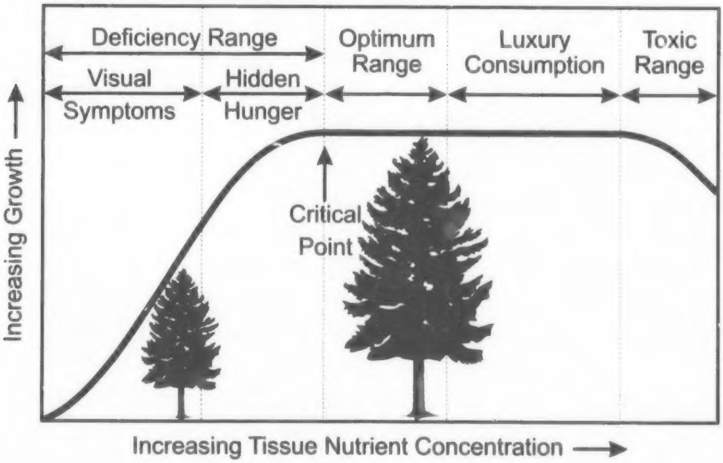


Table 2.3.3. Required nutrient concentrations, metabolic roles, and deficiency symptoms of essential elements for spruce species.

Element	Nutrient concentration required for optimum growth						Metabolic role[g]	Deficiency symptoms
	Conifers[a]	S_b[b]	S_r[c]	S_s[d]	S_n[e]	S_w[f]		
Nitrogen (%)	1.8–3.0	1.5–2.5	1.6–2.8	2.3	1.8	2.5 1.5–2.5[e]	Contained in all amino acids, proteins, chlorophyll molecules, and nucleic acids.	Needle chlorosis followed by stunting; foliage may turn purple and eventual necrosis of leaf tips; older foliage affected first, which leads to red/brown needles.[f,h]
Phosphorus (%)	0.18–0.39	0.18–0.30	0.18–0.28	0.33	0.10–0.30	0.4 0.18–0.32[e]	Part of ATP, nucleic acids, certain proteins, membranes. Involved in the photosynthetic and respiration processes.	Stunting of entire seedling; leaf symptom: purple foliage that gradually turns darker.[f]
Sulfur (%)	0.20–0.27	NA[i]	NA	NA	NA	0.22	Present in amino acids and part of membranes.	Stunting of entire seedling; lower needles first become purple and then turn yellow/brown.[f,h]
Potassium (%)	0.72–1.95	0.4–0.8	0.40–1.10	1.2	0.70–1.1	1.0 0.45–0.80[e]	Important in stomatal movement and enzyme activation.	Stunting of entire seedling; needle tips become golden, near shoot apex, late in season.[f]
Magnesium (%)	0.18–0.25	0.09–0.12	0.08–0.17	0.15	0.09–0.16	0.12 0.10–0.20[e]	Essential to activity in chlorophyll molecules and enzymatic reactions involving ATP.	Yellow or orange tips of current foliage.[h]
Calcium (%)	0.13–0.18	0.10–0.15	0.12–0.30	0.2	0.09–0.60	0.2 0.15–0.40[e]	Important in cell wall structure and membrane function.	Stunting with minimal growth at all meristems.[h]
Iron (ppm)	126–210	NA	NA	NA	NA	50 mg kg^{-1}	Important in the light reaction of photosynthesis and in nitrogen metabolism.	Needle chlorosis appearing first in younger foliage.[f,h]
Chlorine (ppm)	NA	NA	NA	NA	NA	NA	Stimulates light reactions of photosynthesis.	No known symptoms.

Table 2.3.3 (*concluded*).

Element	Nutrient concentration required for optimum growth						Metabolic role[g]	Deficiency symptoms
	Conifers[a]	S_b[b]	S_r[c]	S_s[d]	S_n[e]	S_w[f]		
Manganese (ppm)	72–120	NA	NA	NA	NA	19 mg kg^{-1}	Stimulates light reactions of photosynthesis.	Reduced growth, pale, slightly grey color; needles behind the shoot apex turning yellow over stem length.[f]
Boron (ppm)	3–60	NA	NA	NA	NA	46 mg kg^{-1}	Involved in translocation of sugars.	Stunted growth, terminal buds small or absent; apical needles short, twisted, necrotic.[f]
Zinc (ppm)	5–9	NA	NA	NA	NA	33 mg kg^{-1}	Involved in the synthesis of some amino acids.	Stunted growth; necrotic needle tips near shoot apex.[f]
Copper (ppm)	5–9	NA	NA	NA	NA	15 mg kg^{-1}	Involved in light reactions of photosynthesis.	Needles twisting, with yellowing or bronzing of needle tips.[h]
Molybdenum (ppm)	1.3–2.1	NA	NA	NA	NA	0.5 mg kg^{-1}	Important in nitrogen metabolism.	Needle chlorosis beginning at the tips.[h]

[a] Conifer species assessed included black, Norway, red, and white spruce species (Hallett 1985).

[b] Black spruce (Stewart and Swan 1970).

[c] Red and white spruce species (Swan 1971).

[d] Sitka spruce (van den Driessche 1969).

[e] Norway spruce (Ingestad 1962).

[f] White spruce (van den Driessche 1989).

[g] Salisbury and Ross (1992).

[h] Landis et al. (1989).

[i] NA, no available information.

2.3.4 Visible deficiency symptoms

Deficiencies and excesses of individual elements produce characteristic effects on various organs of plants: foliage characters, including color, density, size, and shape of leaves; stem characters, such as thickness, color, and length of internodes; root characters, such as color, fibrosity, and abnormal thickening (Wallace 1961). Such characteristic effects, however, are clearly expressed only when the metabolic disturbance is caused by deficiency of a single nutrient element. Points at which nutrient deficiency cause metabolic imbalance and produce visible symptoms vary both with species and populations within a species (Smith and Goddard 1973). A description of visible mineral nutrient deficiency symptoms for spruce are found in Table 2.3.3.

In leaves, chlorosis, necrosis, and premature senescence are typical symptoms of mineral deficiencies (Sprague 1964). Chlorosis of spruce has often been regarded as an indicator of N deficiency (Weatherell 1953; Leyton 1954), but any of several other deficiencies may produce the same effect (Ingestad 1960). On the other hand, mature and semi-mature conifers showing no symptoms of deficiency commonly respond by increased volume increment to N fertilization (Morrison and Foster 1990). Visual symptoms of P deficiency in conifer foliage appear only at very low levels, thus making P deficiencies extremely difficult to diagnose. In nature, visual symptoms are seldom distinctive enough to be of diagnostic value in identifying specific deficiencies.

Another factor complicating the understanding of the influence of nutrients on the performance of spruce seedlings is the interaction of various nutrients on performance. If more than one nutrient is in short supply, the application of any one of these may produce no growth response or even a negative response when, for example, ions from an added nutrient displace ions of other nutrients already in short supply. For example, Norway spruce height increment was reduced when N and P were applied without K (Franz and Baule 1962). In another example, average height increment of Norway spruce growing on a raised bog doubled when fertilized with Ca plus P, while it was appreciably reduced when only Ca was applied (Attenberger 1963).

If a nutrient is in a luxury supply, it may cause deficiency symptoms in other nutrients and limit seedling growth. Aronsson (1983) indicated that a sustained macronutrient fertilization of spruce can induce deficiencies of other nutrients (i.e., nutrient antagonism). For plants in general, an excess of N can induce a deficiency in K, S, Ca, Mg, Fe, or Cu, an excess of P can induce a deficiency in N, Mg, Fe, Cu, or Zn, while an excess in K can induce a deficiency in N, Ca, or Mg (Ethrington 1982; Landis et al. 1989). The following are a number of examples of nutrient antagonism in spruce species. In a study on interior spruce seedlings growing in the nursery, a portion of the population exhibited low K concentrations and K deficiency symptoms, took longer to flush, and had less shoot extension than normal green seedlings (van den Driessche and Ponsford 1995). This was attributed to the fact that these seedlings also had greater N content. A heavy N fertilization of these seedlings had created greater requirements for K above concentrations normally regarded as adequate. In other examples, applying N to seedlings caused a reduction in P and K in Norway spruce (Seith et al. 1996) and P in white spruce (Teng and Timmer 1994), which resulted in restricted growth. This nutrient antagonism phenomenon was attributed, in part, to a dilution effect due to increased shoot growth stimulated by increased N level, and because of an insufficient uptake of other ions by the root systems to meet the higher nutritional demand (Teng and Timmer 1995; Seith et al. 1996). These examples show the difficulty in trying to ascribe nutrient deficiency symptoms of spruce seedlings to just one nutrient or an assumed nutrient concentration effect.

2.4 Freezing tolerance

Freezing tolerance is defined as the tolerance to subfreezing temperatures, in other words, the lowest temperature below the freezing point that a tissue can be exposed to without damage. Spruce species can have a wide range in the level of winter freezing tolerance that they develop. The freezing tolerance ranged from –20 to –70°C for needles and winter buds of 40 spruce species surveyed from throughout the world (Sakai 1983). In a survey of trees across North America, boreal spruce species generally develop extreme levels of freezing tolerance in midwinter (i.e., ability to withstand exposure to –80°C), and are some of the most hardy conifer species (Sakai and Weiser 1973). In contrast, Sitka spruce, which naturally grows in the coastal forests of the Pacific Northwest, and red spruce, which grows in eastern North American forests that can range to more southern latitudes, only develop moderate levels of freezing tolerance in midwinter (i.e., –35 to –50°C) (Sakai and Okada 1971; Strimbeck et al. 1995). An example of the difference in the fall development of freezing tolerance for Sitka and interior spruce is presented in Section 4.1. This section briefly covers a number of basic concepts related to the development of freezing tolerance in spruce species. A detailed discussion of spruce seedling response to freezing tolerance throughout the year is found in Section 3.7. Readers should consult Sakai and Larcher (1987) for further details on the basic concepts of freezing tolerance.

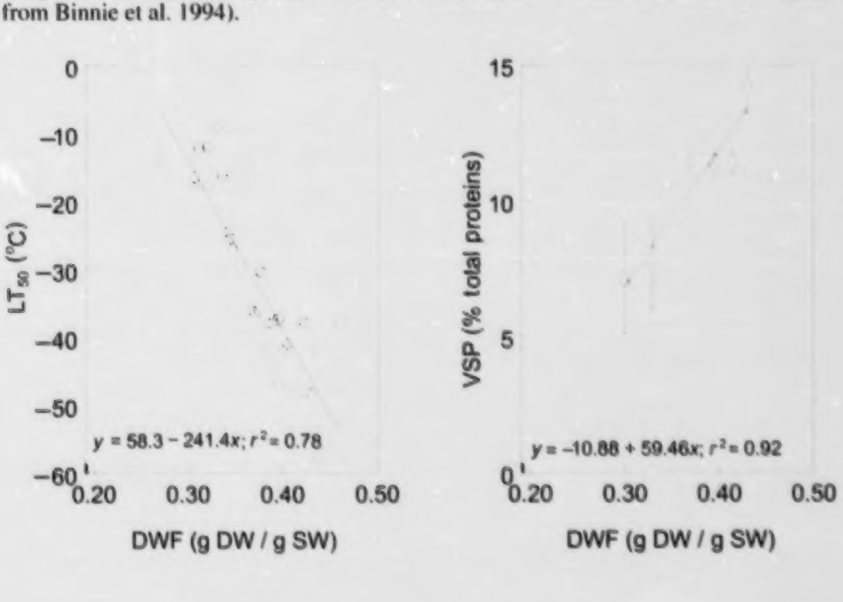
Two types of freezing occur in plants based on the location of ice crystallization. First, extracellular, or extraorgan freezing occurs when ice crystals form outside the cells within the intercellular spaces. This occurs when water is translocated from inside the cells to ice nucleation centers outside the organs. This phenomenon is reported to occur in spruce species (Pukacki 1987). Extracellular freezing predominates in nature and is not lethal to hardy tissue. During this process, water migrates from cells due to ice crystal formation external to cells but in intracellular spaces internal to plant tissues. This extracellular freezing process causes intracellular dehydration that can sometimes cause tissue damage, which plants normally survive. Under these conditions, the "living tissue" becomes dehydrated, i.e., dehydration-tolerant, so that there is no freezable water within the tissue. In this condition, shoot tissue of conifer species from the boreal region can even tolerate temperatures below –100°C (Sakai and Larcher 1987). Second, intracellular freezing occurs when ice crystals form inside cells.

Intracellular freezing disrupts cell membranes through the fast growth of ice crystals inside the protoplasts. In spruce species, this disturbance of the cell membranes is irreversible and leads to death of the tissue (Pukacki and Pukacka 1987). Plants can only survive intracellular freezing when the ice crystals that form are of a fine ice crystal structure that melt before they reach a harmful size (Sakai and Larcher 1987).

Plants have a combination of physiological mechanisms that enable them to tolerate freezing temperatures. Freezing tolerance in plants, under natural conditions, is defined as a tolerance to extracellular freezing (Levitt 1980). The development of freezing tolerance in spruce species is due to a combination of changes in tissue water content, cell solute concentration, and membrane permeability during the fall acclimation process. Spruce species use a combination of these physiological mechanisms to survive subfreezing temperatures.

Increased freezing tolerance of spruce species is accompanied by a decrease in shoot water content of the shoot tissue (Colombo 1990; Calmé et al. 1993). An increase in freezing tolerance of interior spruce seedlings was accompanied by an increase in the shoot dry weight fraction (Fig. 2.4). This decrease in tissue water content increases freezing tolerance through the concentration of cell sap and the reduction of symplastic water volume (Sakai and Larcher 1987). In interior spruce seedlings, this increase in dry weight fraction is partly attributed to the accumulation of vegetative storage proteins (Fig. 2.4). Low molecular weight proteins represent part of the dry matter accumulation that contributes to an increase in freezing tolerance during fall acclimation (Guy 1990). These vegetative

Fig. 2.4. Changes in freezing tolerance (LT_{50}) and vegetative storage proteins (VSP) in relation to dry weight fraction (DWF): grams dry weight (DW) / grams saturated weight (SW) for interior spruce seedlings during the fall acclimation process (adapted from Binnie et al. 1994).



storage proteins are a measure of reserves that are being accumulated in cellular organelles which consequently exclude water and result in a decrease of the water content of shoot tissue.

Vegetative buds of spruce species also have the ability to adjust water content to increase freezing tolerance; this, as well, is achieved through extracellular freezing. For example, water migrates in winter buds of spruce species from shoot primordia to outside nucleation centers (i.e., bud scales and basal parenchyma) (Sakai 1979). It is thought that the smaller size of spruce primordial shoots permits this rapid ice segregation, thereby increasing the rate of water flow out of the tissue and enhancing the ability to tolerate freeze dehydration (Sakai 1983).

Extracellular freezing enables the shoot tissues of spruce species to survive in subarctic regions where winter air temperatures can drop to –50°C (Section 1.2.1) because shoot tissues can survive intensive freeze dehydration from –70 to –80°C or lower temperatures (Sakai and Weiser 1973; Sakai 1983). This mechanism has no low temperature limit, provided that shoot tissues can resist intensive dehydration (Sakai 1979, 1983). Thus, boreal conifers demonstrate enhanced freezing tolerance, as "living shoot tissues" translocate water out of cells and are able to tolerate intensive freezing dehydration.

Increased freezing tolerance of spruce species in the fall is accompanied by a decrease in the osmotic potential (i.e., more solutes) of shoot tissue (Section 2.1.1). Solute accumulation is important in improving freezing tolerance through (*i*) the metabolic effects whereby sugars are metabolized to produce other protective substances or energy and (*ii*) cryoprotective effects involving the protection of cells and biomembranes (Sakai and Larcher 1987). For spruce species, an increase in needle soluble sugar content in the fall parallels the increase in freezing tolerance of shoots (Parker 1959; Aronsson et al. 1976; Amundson et al. 1993). Both active and passive solute accumulation are another means of the acclimation process to freezing temperatures.

Increased freezing tolerance in spruce species occurs as a result of changes in the permeability of membranes. Acclimation to freezing temperatures involves both chemical and structural alterations of the cell membrane to resist freezing dehydration, mechanical stress, molecular packing, and other events caused by extracellular freezing (Sakai and Larcher 1987). There is a belief that the disruption of the cell membrane is the primary cause of freezing injury in plants (Steponkus 1984).

Lipids are an essential component of the cell membranes and are present in a liquid state at warm temperatures (Sakai and Larcher 1987). When temperatures decline, membranes undergo a phase transition from liquid crystalline to a solid state, which increases the susceptibility to stress. Plants that are hardy to low temperatures increase their membrane lipid content (i.e., primarily phospholipids), which significantly increases their winter hardiness (Sakai and Larcher 1987). For example, the membrane lipid composition of winter-hardened Norway spruce needles is almost twice that of freezing sensitive spruce needles

(Senser and Beck 1984). Senser and Beck (1982) postulated that Norway spruce needles undergo a two-step process that changes lipid metabolism during fall acclimation. First, short days trigger an augmentation of membrane lipids (i.e., phospholipids). Second, sub-zero temperatures result in the incorporation of polyunsaturated fatty acids into the membrane lipids. This increase in the membrane lipid content during the winter is important in maintaining membrane fluidity, which ensures their structural and functional stability under freezing temperatures.

The various morphological structures of spruce species have varying degrees of freezing tolerance. In the shoot structure of most conifers, buds usually have a moderate level of freezing tolerance, while the needles, branches, and stems have the greatest level (Sakai and Larcher 1987). However, the freezing tolerance of various plant structures changes seasonally. In the fall, 2-year-old needles of Sitka spruce have a greater level of freezing tolerance than 1-year-old needles (Redfern and Cannell 1982; Jalkanen et al. 1998), although shoot systems of both ages have comparable levels of freezing tolerance throughout the winter and spring (Jalkanen et al. 1998). In midwinter, the buds of boreal spruce species have been reported to withstand temperatures below –70 to –80°C (Sakai 1979), while needles withstand temperatures of –60 to –80°C (Section 3.7). During the spring, spruce buds must have the most rapid loss in freezing tolerance because they are reported to be the most susceptible shoot tissue to late-spring frosts (Clements et al. 1972). After budset, spruce buds quickly develop freezing tolerance and are hardier than shoot tissue because seedlings exposed to late-summer frost can have severe needle damage yet are still capable of budbreak and shoot growth the following spring (S. Grossnickle, unreported data). This seasonality in freezing tolerance of various shoot forms indicates that protection of spruce seedlings needs to be based on the most susceptible shoot tissue for any given season.

The root systems usually have the least freezing tolerance of all plant structures (Sakai and Larcher 1987). For spruce seedlings, there seems to be gradual change in freezing tolerance between the shoot and root system, with the highest level of freezing tolerance occurring from the top of the shoot system to the least level at the root tip (Southon et al. 1992; Colombo et al. 1995). The general reduction in freezing tolerance down through the root systems indicates that seedling root systems need to be protected from severe frost events.

Freezing tolerance of conifers is influenced by seasonal changes in environmental factors such as temperature and light (Weiser 1970; Sakai and Larcher 1987). The freezing tolerance response of spruce to changes in seasonal environmental parameters are explored in Section 3.7. Seasonal changes in freezing tolerance are also influenced by the phenological cycle of spruce species (Sections 3.7 and 3.9).

2.5 Dormancy

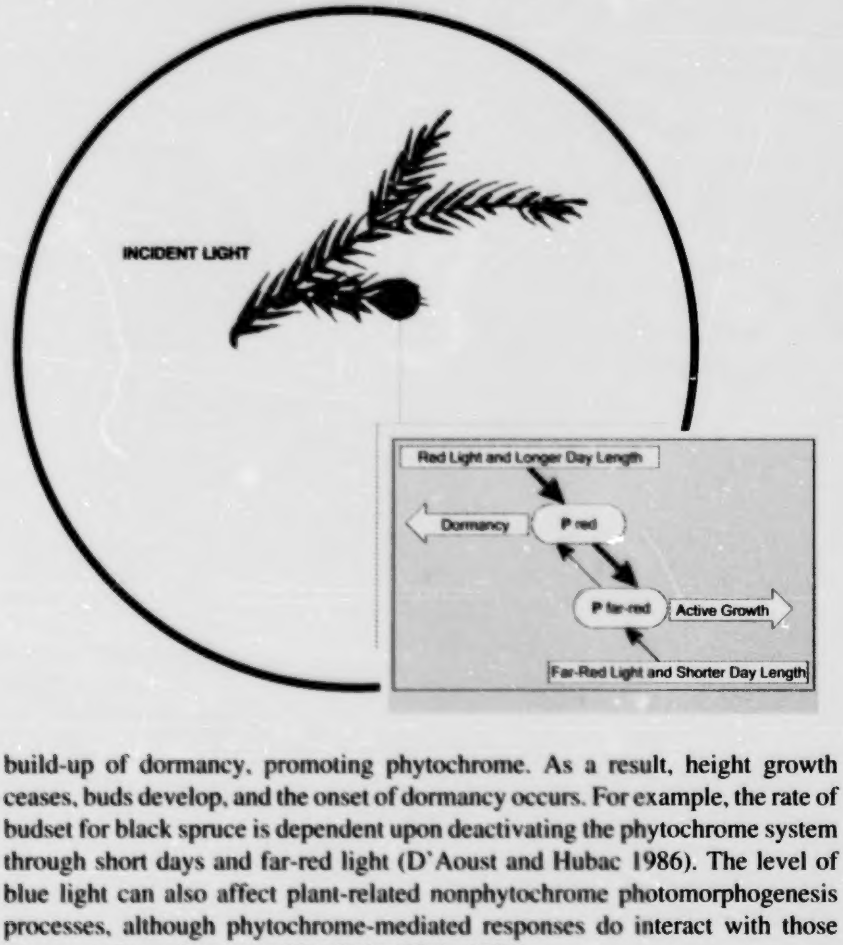
Dormancy occurs "when an organ or tissue, predetermined to elongate or grow in some other manner, does not do so." (Doorenbos 1953). Thus, dormancy results in a temporary suspension of growth and development. In woody temperate perennials, dormancy is restricted to the apical meristems (Lavender 1991). Spruce species are generally considered dormant when terminal buds have formed on shoots. The following section describes principles of dormancy that are important in understanding spruce seedling performance. Readers should consult Lavender (1985, 1991) for more information on dormancy in conifer species.

Dormancy and the growth phase are parts of the phenological cycle of spruce species. Spruce seedling phenology is related to the timing of periodically reoccurring physiological processes and their relation to the environment. Dormancy in spruce species is confined to the apical meristems and has three stages: quiescence, rest, and postdormancy. Quiescence is the earliest stage of dormancy commonly occurring in mid- to late summer. In this stage, growth is controlled by a number of environmental factors (i.e., photoperiod and thermal inputs), not by internal plant physiology. Thus, a spruce seedling grows, during this phase, if environmental conditions allow growth to occur. The rest phase occurs in the fall season. In this phase, growth is controlled by bud physiology. Even under favorable conditions, growth does not occur due to a state of unfavorable internal physiological conditions. In the postdormancy phase, growth is again controlled by the environment (i.e., photoperiod and thermal inputs) rather than bud physiology.

Changes in the photoperiod influence the vegetative phase of spruce seedling growth. As previously discussed, the lengths of day and night are dictated by the annual revolution of the earth around the sun, and the higher latitude location of the boreal forest (Section 1.1.4). Photomorphogenesis is the process by which radiation affects the plants at the subcellular, cellular, and whole-organism level. Photomorphogenesis synchronizes the development and the rhythmic events in the life cycle of a plant through changes in the diurnal light and dark patterns and seasons of the year.

These photomorphogenesis processes are triggered by the phytochrome system, which is a light-receptive protein pigment complex found in the tissue of plants (Kramer and Kozlowski 1979). The phytochrome system triggers changes in spruce species dormancy phases in relation to day length. An important aspect of phytochrome regulation is the ratio of the two forms of phytochrome, as this ratio is always in a dynamic state of flux, depending upon changes in light quality and day length (Fig. 2.5*a*). Light in the red part of the spectrum (640–740 nm) acts on the phytochrome system to change it into a form that promotes biological processes related to active growth and development. Far-red light (740–800 nm) changes the phytochrome system back into a state that promotes biological processes related to bud development and dormancy. In the dark, the phytochrome form that promotes active growth and development slowly reverts to the form that promotes dormancy. If day lengths are long enough, the amount of growth promoting phytochrome that undergoes dark reversion is small, and seedling growth continues to occur. When day length becomes short enough, there is a

Fig. 2.5a. Absorption of red light and longer day lengths convert the pigment phytochrome red (the inactive form) back to phytochrome far-red (the active form), which promotes active growth and development. In contrast, the absorption of far-red light and shorter day length convert the pigment phytochrome (far-red) back to phytochrome (red), causing dormancy. The phytochrome pigment complex is most abundant in meristematic tissue cells of growing points of plants.


INCIDENT LIGHT
Red Light and Longer Day Length
Dormancy
P red
P far-red
Active Growth
Far-Red Light and Shorter Day Length

build-up of dormancy, promoting phytochrome. As a result, height growth ceases, buds develop, and the onset of dormancy occurs. For example, the rate of budset for black spruce is dependent upon deactivating the phytochrome system through short days and far-red light (D'Aoust and Hubac 1986). The level of blue light can also affect plant-related nonphytochrome photomorphogenesis processes, although phytochrome-mediated responses do interact with those processes dependent upon blue light (Mohr 1994).

Very low light intensity is required to trigger the photomorphogenesis process. For spruce species, shoot growth continues with exposure to only 8 μmol m^{-2} s^{-1} (Tinus and McDonald 1979; Arnott and Macey 1985). Above this critical minimum light intensity, the phytochrome form that is produced promotes biological processes related to active growth and development of spruce species. This is why both normal daytime light levels and the low light levels that occur around sunrise and sunset, as day length changes during the growing season, are critical to the shoot growth patterns of spruce seedlings.

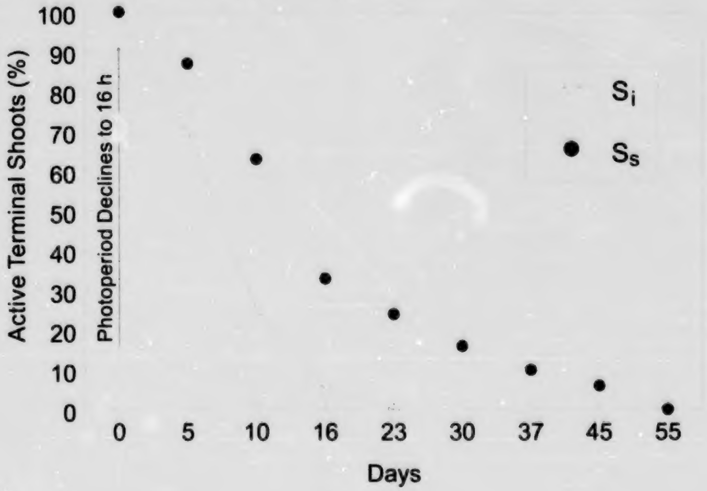
Bud development for spruce species during the growing season is triggered by a shortening in length of the photoperiod as summer progresses (Section 1.1.4). Day length is considered the predominant environmental factor influencing growth cessation and the onset of dormancy in spruce species (Dormling et al. 1968; Leikola 1970; Heide 1974*a*; Aronsson 1975). For example, Norway spruce from northern latitude sources (~66° N lat.) initiated bud development at 19 h compared to ~17–18 h for white spruce (~60–64° N lat.) and 12–16 h for Sitka spruce (~58–60° N lat.) (Junttila and Skarat 1990). White and Sitka spruce populations from a more southern latitude (~50° N) initiated bud development at a photoperiod of 16–17 h during the summer (Roche 1969), while budset in black spruce seed sources used for reforestation in Ontario (i.e., collected from ~48–50° N lat.) usually occurred at photoperiods less than 14 h (Colombo et al. 1982; Colombo 1997). The photoperiod at which spruce species set bud is related to both latitude and elevation of their origin. This topic is discussed later in the treatise (Section 4.2).

The photoperiod stimuli may be modified by decreasing temperatures (Cannell et al. 1976). For example, black spruce set bud earlier under cold, compared to warm, temperatures (Morgenstern 1976), while Norway spruce seedlings grown under continuous light set bud after exposure to a cold temperature treatment (Heide 1974*a*). Thus, it is the combination of day length and decreasing temperatures that triggers bud development for spruce species in the fall. Otherwise, spruce species would set bud at exactly the same date each year, which does not occur.

Spruce species from the same geographic region or latitude can have differing strategies in the way in which they end the seasonal growth period and start to set bud. For black and white spruce sources selected from the same region in Ontario, white spruce had growth cessation up to 10 days earlier than black spruce, indicating that the two species have different budset requirements (O'Reilly and Parker 1982). Budset in Sitka spruce (i.e., collected from 58 to 60° N lat., elevation 10–120 m) had a critical photoperiod shorter than 16 h compared to 17–18 h for white spruce from a comparable latitude and elevation (i.e., collected from 61° N lat., elevation 20 m) (Junttila and Skaret 1990). Junttila and Skaret (1990) speculated that white spruce may respond to changes in light quality in a different manner than other spruce species. In a study comparing the budset patterns of interior and Sitka spruce, the entire interior spruce population set bud within 23 days, while the entire Sitka spruce population set bud 55 days after exposure to photoperiods of less than 16 h (Fig. 2.5*b*). This rapid rate of budset in the interior spruce population indicates that once the declining photoperiod cues the population for growth cessation and the onset of dormancy, this spruce species responds quickly, probably as a means to avoid any potential late-summer frost events that can occur on northern latitude / continental forest sites.

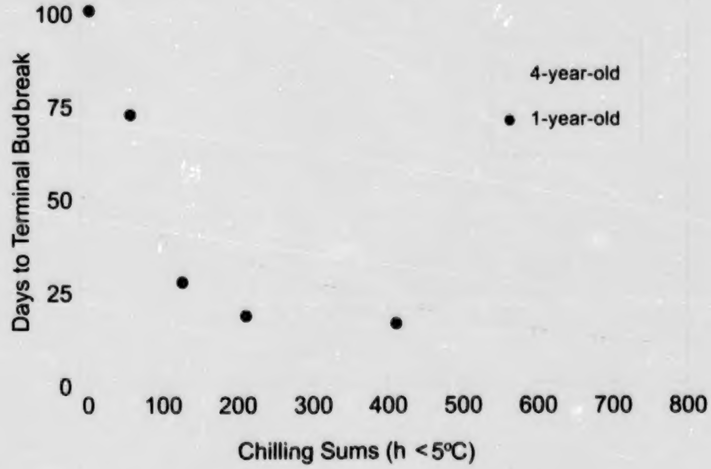
Dormancy can only be reversed if spruce species are exposed to a series of environmental cues that move them through the various dormancy phases. The environmental cues are primarily temperature and seasonal photoperiod. Each

Fig. 2.5*b*. The length of time required for the entire population ($N = 120$) to complete budset for an interior (S_i; lat. 53°30′ N to 55°40′ N) and Sitka (S_s; lat. 54°10′ N) spruce population (S. Grossnickle, unreported data).



species has its own temperature and time requirement; this is termed the chilling requirement. Temperatures of about 5°C for approximately 6 weeks cause the transition from rest to postdormancy in white spruce (Fig. 2.5*c*). However, there was a difference between 1- and 4-year-old seedlings during the stage of quiescence in late summer. One-year-old seedlings that had just gone through their first indeterminant growth stage of bud development required nearly twice as

Fig. 2.5*c*. The number of chilling hours required to break terminal buds of 1- and 4-year-old white spruce seedlings during fall acclimation (adapted from Grossnickle 1989 and Grossnickle et al. 1994).



many days to break bud than 4-year-old seedlings. With just 100 chilling hours, this high level of number of days required to break bud decreased rapidly, and thereafter, the number of days to budbreak was comparable between 1- and 4-year-old seedlings. Nienstaedt (1967) found that for a range of spruce species the initial 336 h of chilling were relatively more effective than are subsequent additional hours of chilling for 1-year-old seedlings.

The cumulative hours of chilling (<5°C) required to overcome the rest phase of dormancy is generally between 750 and 1300 h for young (Nienstaedt 1967; Ritchie et al. 1985; Grossnickle 1989; Silim and Lavender 1991) and mature (Nienstaedt 1966) spruces. Unless spruce seedlings remain dormant in the fall, they reflush during warm spells and are susceptible to frost damage during nights with freezing temperatures. Nienstaedt (1967) speculated that this chilling requirement, or rest phenomenon, in spruce is an adaptive trait associated with the protection it gives this genus against early fall frosts.

The release of dormancy during the fall that occurs with the accumulation of chilling hours can sometimes be nullified by warm temperature events. In Norway spruce, the rest breaking effects of cumulative chilling temperatures were nullified when intermittent warming events occurred during the latter portion of the fall chilling period (Hänninen and Pelkonen 1989). This indicates that warm temperatures in the fall can alter the dormancy development pattern in spruce species and might cause delays in proper development of seedling hardiness (Section 3.9). The interruption of fall dormancy development can be especially critical when spruce seedlings are grown in nurseries that are at more southern latitudes in comparison to regions where seed was collected. This might cause delays in the proper development of seedling hardiness required for timing the successful lift to frozen-store seedlings over winter (Section 5.1.3).

Once chilling requirements are met, spruce species move from rest phase to postdormancy or quiescence. At this point, they are able to break bud when environmental conditions allow. The duration of dormancy through late winter and into the spring is controlled by low air temperatures (Havranek and Tranquillini 1995), while budbreak in the spring for spruce populations is predominantly controlled by warm air temperatures (Roche 1969; Aronsson 1975; Owens et al. 1977; Cannell and Smith 1983). After plants have reached postdormancy during the late fall or winter, the number of hours >5°C (i.e., thermal time) recorded during the subsequent winter and spring determines when budbreak occurs in white (Owens et al. 1977), Sitka (Cannell and Smith 1983), and Norway (Hannerz 1999) spruce populations. Under optimum, and continuous, environmental conditions (i.e., temperature at 20°C, 20 h photoperiod, well-watered), interior spruce seedlings needed only 350–500 h of thermal time to break bud (Fig. 2.5*c*). Pollard and Ying (1979*b*) also found white spruce seedlings (range of populations from ~44 to 46° N lat.) needed only 350–500 h of thermal time to break bud under similar optimum environmental conditions. Interior spruce requires 1300 h of thermal time, while Sitka spruce requires over 1900 h of thermal time for 80% of the population to break bud under field conditions (Fig. 4.1*a*, Section 4.1). The average date for flushing of white spruce was 9 days ahead of black spruce selected from the same region in Ontario (O'Reilly and Parker 1982). O'Reilly and Parker (1982) speculated that this could be why white spruce is more susceptible to spring frost events than black spruce, a species that generally does not get damaged by frost.

Other environmental factors may also play a role in the budbreak of spruce species in the spring. The combination of fluctuating day/night temperatures, compared to a constant temperature, to accumulate thermal time and continuously lengthening photoperiod promoted the shortest time to budbreak in Norway spruce (Partanen et al. 1998). Both low temperatures during growth cessation (Malcolm and Pymer 1975) and photoperiods of increasing length in the spring (Worrall and Mergen 1967) can advance the date of budbreak in spruce seedlings. It has also been suggested that the timing of flushing in white spruce is related to the last regional occurrences of spring frosts (Pollard and Ying 1979*b*). In contrast, photoperiod and soil temperature have not been found to have any major effect on budbreak of Sitka spruce in the spring (Cannell and Smith 1983). It is realistic to expect that other environmental cues (e.g., diurnal temperature range, photoperiod, soil temperature, soil water) interact with thermal time to define when spruce species break bud in the spring.

2.6 Morphological development

Spruce seedlings can achieve dominance through the ability to grow rapidly and fully exploit the environment on a reforestation site. The interactions of growth strategies for spruce seedlings and the competing vegetation determines whether a successful forest plantation is established. In this section, the patterns of morphological development for spruce seedlings are discussed. The influence of environmental conditions on growth are examined in Section 3, and the interaction of spruce growth patterns in relation to reforestation site conditions is part of the discussion in Section 5.

2.6.1 Shoot development

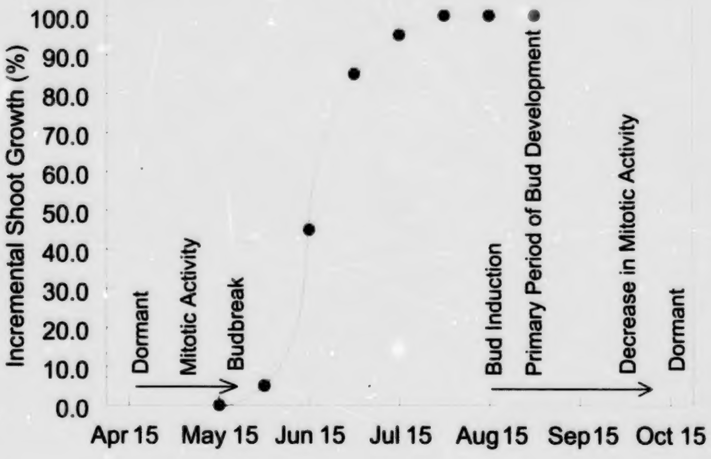
2.6.1.1 Shoot growth

Shoot growth in conifers involves both leader growth (the lengthening of the shoot) and needle tissue production. This process is influenced by four centers of cell division and expansion: (*i*) shoot apices (where new stem units and potential needles are produced), (*ii*) subapical meristems (which regulate the subsequent elongation of the internode at each stem unit), (*iii*) needles, and (*iv*) sites at which new lateral vegetative apices can form (Cannell et al. 1976). The lengths attained by stem units on woody plants are often due more to differences in cell numbers than to differences in cell length (Cannell et al. 1976). Environmental conditions that cause water stress can limit cell division and expansion from occurring and can reduce shoot growth (Section 3.5.2.1).

Vegetative buds of spruce species go through three phases during the seasonal developmental cycle: (*i*) a resting or dormant phase, (*ii*) a period of shoot elongation and bud scale formation, and (*iii*) needle primordia formation (Owens and Molder 1976, 1977; Harrison and Owens 1983). During the dormant phase, buds show no mitotic activity (i.e., cell division), and this dormant phase can extend for up to 6–7 months. In the 4–6 weeks prior to budbreak, mitotic activity starts in the buds of various spruce species (Owens and Simpson 1988; Hejnowicz and Obarska 1995; Westin et al. 1999) (Fig. 2.6.1.1*a*). Just prior to budbreak in the spring, lateral buds that develop into future whorl and interwhorl branches are produced by differentiation of areas of cortical tissue between the needle primordia (Cannell et al. 1976). Buds that seem to be dormant are physiologically active during this early spring period.

When buds break in spruce species during the spring, basal stem units elongate ahead of apical stem units, with the elongating shoot consisting of stem units in different stages of elongation (Cannell et al. 1976). During this shoot elongation phase, the shoot apical meristem region produces new stem units, which either are used to build buds, which overwinter and elongate the following year as fixed growth, or if the stem units are formed early in the current season, are used in a second growth flush, called free growth (discussed below) (Cannell and Willet 1975; Owens and Molder 1976, 1977). The rate of shoot elongation fluctuates in response to current environmental conditions because cell division and elongation are very sensitive to drought stress, air temperature, and incoming solar radiation (Ford et al. 1987*a*). These young, developing shoots import considerable quantities of photosynthates (Kramer and Kozlowski 1979). The availability of these photosynthates is tied to the photosynthetic response to field

Fig. 2.6.1.1*a*. Representation of shoot development for white and Engelmann spruces grown at 54° N lat. (compiled from Owens et al. 1977; Harrison and Owens 1983). Shoot phenological stages are defined by mitotic activity, budbreak, bud induction, bud development, and the dormant phase.



site environmental conditions (Section 3). In this way, shoot development in the spring and summer is directly linked to environmental conditions at the field site.

Shoot elongation in spruce species usually occurs during a certain period of the growing season. The initial 1–2-week stage of shoot elongation is usually slow and is followed by a rapid flush of growth from preformed stem and needles, with 60–70% of the seasonal shoot elongation occurring over a 4-week period (Fig. 2.6.1.1*a*). During this period of rapid shoot growth, the extension rate can reach a maximum of 3.5 mm day^{-1} in Sitka spruce (Ford et al. 1987*a*), while Norway spruce (calculated from Heide 1974*a*) and Engelmann and white spruces (calculated from Arnott and Macey 1985) were estimated to have an average shoot growth rate of 1.9, 2.3, and 2.0 mm day^{-1}, respectively. Continued shoot elongation can occur in seedlings if free growth allows for the development of nonpreformed new needles (see below for discussion on the subject of free growth) (Jablanczy 1971). The entire period of shoot growth for northern latitude spruce species growing in continental climates (e.g., Engelmann and white spruces) lasts for 8–12 weeks (Owens and Molder 1976, 1977). Other work has also reported that the period of shoot growth can range from 6 to 7 weeks in black and white spruces grown at a latitude of 48° N in Ontario (O'Reilly and Parker 1982). For Sitka spruce, the period of shoot elongation varied between whorls along the shoot system, with upper whorls and the leader growing for 9 weeks and whorls lower down on the shoot system growing for 7.5 weeks (Ford et al. 1987*b*). Hellum (1967) found white spruce seedlings (from 54° N lat.) grew in height over a 4–9-week period, with seedlings that had the longest period of growth also having the greatest new shoot length. The length of the shoot elongation period is tied to environmental conditions of the field site (noted above). In addition, the cessation of shoot growth and initiation of bud development is triggered by the seasonal pattern of reduced length in photoperiod and decreased temperature in late summer (Section 2.5). Spruce species seem to have a general time during the growing season when shoot growth occurs, but the final length of time is determined by both site and seasonal environmental conditions.

The initial spring flush of shoot growth is the result of stem units developed in the previous late spring, summer, and early fall, while free growth is the elongation of stem units formed during the months when growth actually occurs (under optimum conditions during early to midsummer) (Cannell et al. 1976). This process of free growth is common in young spruce seedlings. The percentage of free growth, in relation to total seasonal shoot growth, ranges from 43% in black spruce (Colombo 1986), 16–21% in Norway spruce (Ununger et al. 1988), and 10–33% in white spruce (Macey and Arnott 1986) seedlings during their second year of growth. Free growth among different genetic sources can be up to 37% of predetermined growth for black spruce (Pollard and Logan 1974) and up to 22% in Sitka spruce (Mboyi and Lee 1999) in 4-year-old seedlings.

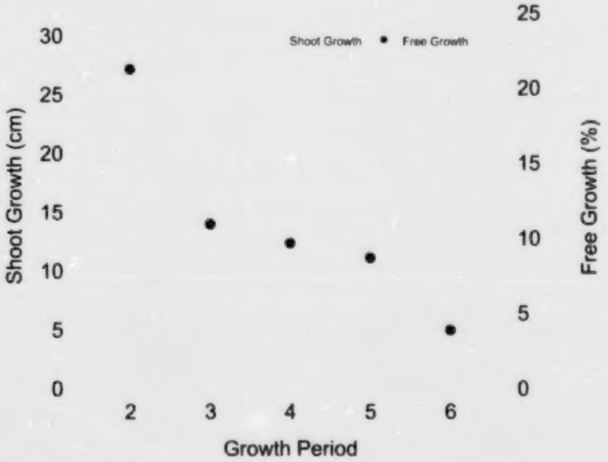
There is inconsistent evidence for the relationship between free growth, predetermined growth (i.e., through bud development), and their effects on the following year's growth in spruce species. Cannell and Johnstone (1978) found that the free growth period in Sitka spruce utilizes stem units that would have gone into bud development for the next year's fixed growth, thereby reducing the number of stem units that go into bud development. On the other hand, the free growth and bud development phases were found to be independent of one another in black spruce (Pollard and Logan 1974). In Norway spruce, free growth during one year did not encroach on the period of predetermined growth, but instead increased the amount of predetermined growth (Ununger and Kang 1988). In white spruce, the amount of free growth that occurs appears to be a compensative rather than an additive effect; that is, seedlings that were shorter in height growth in the previous year had greater free growth in the second year under optimum environmental conditions (Macey and Arnott 1986). Further clarification is required of this relationship between predetermined and free growth in one year and growth during the following year in spruce seedlings.

The prevailing photoperiod and temperature determine whether or not free growth, and the length of this free growth event, occurs in spruce (Cannell et al. 1976; Pollard and Logan 1977). Varying reports on the relationship between predetermined and free growth on subsequent shoot growth patterns are related to environmental conditions seedlings are exposed to when these shoot growth events take place. For example, the free growth period in Norway spruce seedlings was directly tied to favorable growth conditions during the summer shoot growth phase (von Wuehlisch and Muhs 1991). In another example, Sitka spruce progeny had a better expression of free growth on a favorable site, while there was less of an expression of free growth on less favorable sites (Cannell and Johnstone 1978). Also, the number of needle primordia formed in the bud is dependent upon environmental conditions seedlings are exposed to during the shoot developmental phase (see below). The potential for free growth in spruce species is tied to the environmental conditions that occur during the late summer and to the age of the plant.

The free growth phase gradually diminishes to zero in spruce species during a period of 5–10 years (Nienstaedt 1966; Jablanczy 1971; Cannell et al. 1976; Ununger et al. 1988). This is due to the increasing portion of stem units being unable to elongate because they are less sensitive to prevailing day length or they are inhibited by the presence of bud scales (Cannell et al. 1976). The loss of free growth enables spruce species to utilize time, formerly spent in free growth, towards development of needle primordia for predetermined shoot growth in the following year (Pollard and Logan 1974). This is why total seasonal shoot growth remained fairly constant over five growth periods in Norway spruce seedlings even though there was a decline in free growth (Fig. 2.6.1.1*b*). The interaction of predetermined and free growth phases can have a marked effect on the shoot development patterns of spruce seedlings as they go through the establishment phase after being planted on a reforestation site.

Shoot growth is critical for planted spruce seedlings to occupy the site and become dominant within the vegetation complex of the reforestation site. However, it is difficult to provide an exact rule of thumb on how much shoot growth

Fig. 2.6.1.1*b*. Incremental shoot growth and the percentage of free growth of Norway spruce seedlings over five growth periods (adapted from Ununger et al. 1988). Seedlings were 20.7 cm (± 0.52) tall with 100% coming from free growth during the first shoot growth period.



can be expected in planted spruce seedlings. In a survey of established spruce seedlings, shoot growth ranged from 7 to 25 cm (Table 2.6.1.1). This range probably represents the maximum rate of shoot growth that can be expected in young spruce plantations. Shoot growth for planted spruce seedlings is dependent upon various nursery cultural and silvicultural practices, and field site environmental conditions. This is why there is such a wide range in maximum shoot growth rates recorded across all of these studies. The following sections of this treatise discuss spruce seedling shoot growth in relation to field site environmental conditions (Section 3), nursery cultural practices (Sections 5.4.1.3, 5.4.6.1, and 5.4.8), initial seedling size (Section 5.4.1.4), stock type (Section 5.4.1.5), and silvicultural practices applied at the field site (Sections 5.4.6.2, 5.5, and 5.6).

After bud induction, needle initiation of spruce species follows, with a rapid phase of development for a period of up to 6 weeks followed by another 4-week period of slower development (Pollard 1974*a*; Owens and Molder 1976, 1977) (Fig. 2.6.1.1*c*). The number of needle primordia formed in the terminal buds of spruce seedlings varies, depending upon a number of environmental variables. Temperature is one of the major factors known to affect bud development in spruce species; cooler temperatures produce buds with fewer needle primordia (Pollard and Logan 1977, 1979; Colombo 1997). Soil water can also affect bud morphogenesis with low soil water potential (i.e., $\Psi_{soil} < -0.5$ MPa), causing a reduction in needle primordia development (Pollard and Logan 1977, 1979; Macey and Arnott 1986) (Section 3.5.2.1). The effect of light intensity is also a major factor, as the number of needle primordia initiated decline with a decrease in light intensity (Pollard and Logan 1979); a photoperiod of less than 6 h also results in a reduction in needle primordia development (Pollard and Logan 1977).

Table 2.6.1.1. Optimum early height growth of spruce seedlings planted on reforestation sites throughout northern latitude forests.

Spruce species	Stock type[a]	Field age	Incremental height growth ($cm\ yr^{-1}$)[b]	Reference
White	1+0 C	3	~17	Burdett et al. 1984
	1+0 C	3	~12	Wood and Dominy 1985
	1+0 C	2	16	Lautenschlager 1995
	2+1 BR	3	~25	Sutton 1975
	2+0 / 2+1 BR	3	~11	Burdett et al. 1984
	3+0 BR	2	18	Brand 1990
	1+0 C	2	18–20	Groot et al. 1997
Interior	1+0 C	3	10	Vyse 1981
	2+0 / 2+1 BR	3	11	Vyse 1981
Engelmann	2+0 C	3	8	Maze and Vyse 1993
	1+0 C	3	~12	Balisky and Burton 1997
Sitka	1+1 BR	3	~ 24	Mason and Biggin 1988
	BR	3	24	Cochrane and Ford 1978
Black	1+0 C	3	~11	Wood and Dominy 1985
	3+0 BR	3	~18	Sutton 1982
	1+0 C	2	7	Malik and Timmer 1996
Norway	1+0 C	3	~23	von Wuehlisch and Muhs 1991
	1+0 C	2	~7.5	Junttila and Skaret 1990

[a] C represents a container stock type and BR represents a bare-root stock type.

[b] Represents the best incremental height growth of any treatment in the field study.

Low seedling nutrition, as well, can cause a reduction in needle primordia development (Pollard and Logan 1979; Bigras et al. 1996) (Section 3.6.3). These studies indicate that environmental conditions that are less than optimal during bud development have a major effect on needle primordia development, which in turn influences the level of shoot growth the following growing season.

A number of studies have reported that in spruce the number of needle primordia that are formed is related to seedling size; bigger seedlings have a larger number of needle primordia (Pollard 1974*b*; Young and Hanover 1977). However, this phenomenon does not seem to occur in container-grown interior spruce seedlings (Section 5.1.4.2). In general, container-grown seedlings have a range of 150–250 needle primordia in terminal buds (Sections 4.4.1 and 5.1.4). Other work with container-grown spruce seedlings report that terminal buds can form over 200 needle primordia under optimal conditions (Colombo et al. 1982;

Fig. 2.6.1.1*c*. Development of needle primordia in the terminal buds for interior spruce seedlings ($N = 10$: mean ± SE) during the summer in a nursery located in southern British Columbia (S. Grossnickle and R. Folk, unreported data).

Colombo 1997) (Fig. 2.6.1.1*d*). Indications suggest that spruce seedlings with this level of needle primordia development have good shoot growth potential during the first year of shoot elongation on reforestation sites.

During the last phase of needle initiation, mitotic activity of the shoot apex declines. For example, white spruce shows a decrease in mitotic activity to near zero over a period of 12 weeks after bud induction and completion of the primary period for needle initiation (Fig. 2.6.1.1*e*). Mitotic activity of spruce seedlings

Fig. 2.6.1.1*d*. Bud development for container-grown black spruce seedlings (photographs provided by S. Colombo). Median longitudinal section (× 20) of a dormant terminal bud showing the bud scales, needle primordia, apex, and crown region (left). Dissected dormant vegetative terminal bud (× 30) showing the apex and needle primordia (right).

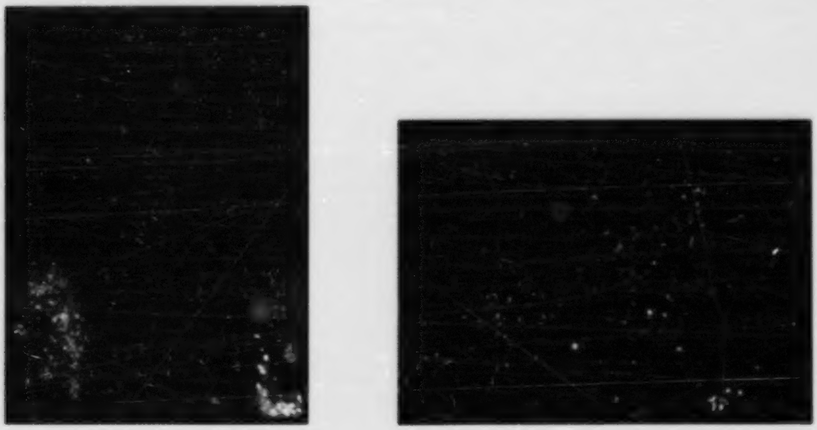
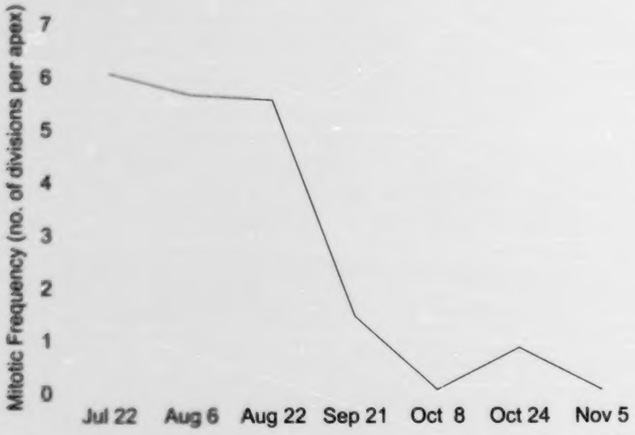


Fig. 2.6.1.1*e*. Mitotic frequency for white spruce during fall acclimation located near Prince George, B.C., (54° N lat.). Bud induction occurred in mid July, with the primary period of needle initiation occurring in August until mid September (adapted from Owens et al. 1977).



also declines to a low level over a 10-week period after bud initiation in the nursery (Colombo et al. 1989; Binnie 1993). The speed at which mitotic activity declines is related to the decrease in fall temperatures. Westin and associates (1999) speculate that a declining photoperiod is also involved in the fall decrease in mitotic activity of Norway spruce. A bud is considered dormant when none of the cells of the embryonic shoot has mitotic activity (Lavender 1985). This dormant bud consists of an embryonic shoot enveloped in bud scales, arising from the stem immediately below the base of the embryonic shoot (Templeton et al. 1993) (Fig. 2.6.1.1*d*). A dormant bud with a full complement of needle primordia is the physiological and morphological state of spruce buds as they go into the winter period.

Shoot growth in spruce species is influenced by both the previous year and current growing season environmental conditions. Needle primordia that represent predetermined shoot growth in the current year are formed in the previous year, thus previous year environmental conditions influence their development (as noted above). current-year growth (i.e., the combination of predetermined and free growth) is influenced by current growing season conditions. Current-year growing season environmental conditions also influence needle primordia development that results in predetermined growth in the next growing season. In this way, spruce seedling shoot growth, in any given year, is always linked to environmental conditions from the previous year.

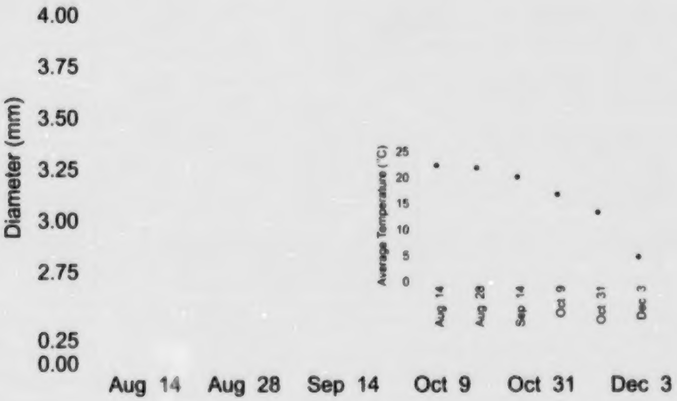
2.6.1.2 Diameter growth

Radial growth in trees occurs primarily from meristematic activity in the vascular cambium. The cambial zone is a cylindrical layer located between the xylem and phloem in the stem, branches, and roots. Radial growth occurs when the cambial zone initiates dividing xylem and phloem mother cells which then enlarge in a radial fashion, with the xylem growing in an inward direction and the phloem in an outward direction. In slow-growing tree species (e.g., spruce), this cambial zone of radial growth is only 4–10 cells in width (Bannan 1962; Zimmerman and Brown 1971). In temperate and boreal forests, the resumption of cambial growth in the spring is associated with the renewed activity of buds and the development of new leaves; with activity first appearing just below buds and moving basipetally along branches and the stem (Zimmerman and Brown 1971). This has led to the theory that auxin, a plant hormone produced in active buds, plays a dominant role, although the interaction of auxin with other plant hormones (i.e., gibberellins and cytokinens) are also important in cambial growth (Kozlowski and Pallardy 1996).

Diameter growth of tree species varies throughout the growing season with environmental conditions. For example, it is generally felt that cambial activity is strongly affected by water availability (Kozlowski et al. 1991), with up to 80–90% of the variation of diameter growth in trees attributable to changes in the plant water status in relation to site water availability (Zahner 1968). This occurs because cell division and elongation are very sensitive to water stress events (Hsiao 1973). In contrast with predetermined shoot growth (see above), diameter growth is affected mainly by environmental conditions during the current year. This is why the exposure of spruce species to limiting environmental conditions during the growing season can reduce diameter growth (Sections 3 and 5.5). For this reason, it is felt that radial growth of conifer species is more sensitive than height growth to environmental changes during the growing season (Zedaker et al. 1987).

The cessation of radial growth in the late summer and fall is tied to field site environmental conditions. In many tree species, the continuation of cambial growth in the fall is linked to continued shoot expansion, while in other species, cambial growth continues after a cessation of height growth and is tied to seasonal temperatures. In the northern latitude forests, the reduction of cambial growth in spruce species seems to be tied to the decline in seasonal air temperatures (Marr 1948; Fraser 1962; Tranquillini 1979). Tranquillini (1979) felt that at cooler temperatures there was a tendency for photosynthates to be transformed to sugars and starch rather than cellulose which limited diameter growth. An example of this is shown with container-grown interior spruce seedlings, growing in a southern British Columbia nursery, that had rapid diameter growth after budset in mid August, with a small but continual increase in diameter through October (Fig. 2.6.1.2). The slowing and then cessation of diameter growth that occurred in these seedlings during October and November coincided with a decrease in air temperature. These findings indicate that spruce species continue to have diameter growth in the fall, after budset has occurred, if environmental conditions are favorable for growth.

Fig. 2.6.1.2. Diameter growth of interior spruce seedlings during the fall in a nursery located in southern British Columbia (adapted from Grossnickle et al. 1994). Budset was initiated in these seedlings in mid August. The insert figure represents the average air temperature for the 2 weeks prior to the first diameter measurement and the average temperature for the period prior to all following measurements.



2.6.1.3 *Shoot system form*

The shoot system of spruce species is affected by both environmental conditions during shoot development and the inherent form of the spruce species. Shoot form consists of the arrangement and structure of needles along the branches, and the arrangement of branches along the stem. The color of spruce needles is related to chlorophyll content, which in turn is affected by location within the crown, season of the year, and environmental conditions. This morphological development strategy and needle color has a direct bearing upon the gas exchange capability of the shoot system.

In spruce, the size, weight, and distribution of needles varies, depending upon their position along the shoot. For example, in Sitka spruce, the largest needles are located near the middle of each year's shoot growth (Chandler and Dale 1990; Wang and Jarvis 1993). This greater needle size is due to a greater number of cells in preformed needles rather than cell elongation during growth. In addition, greater needle internode lengths in Sitka spruce results from greater cell numbers rather than cell lengths (Baxter and Cannell 1978). As a result, the distribution and length of needles along a branch, for each year's shoot growth, is related to the total number of cells that have formed in the apical dome during the previous late-summer and early-fall bud development phase.

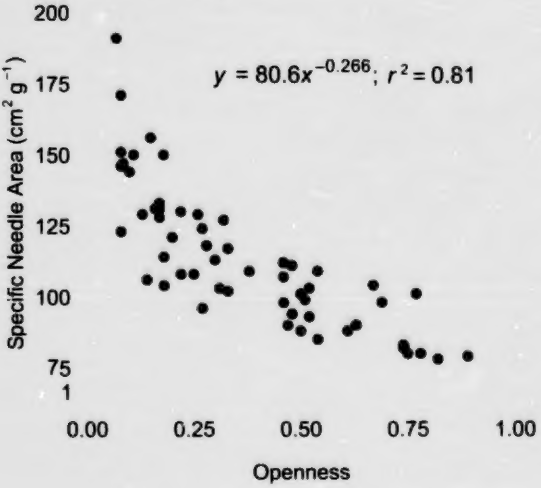
One of the unique characteristics of conifer species is the long-lived nature of the foliage. Needle retention in spruce species is believed to be an adaptive trait to living in low-resource environments. Black spruce needle longevity ranges from only 5 to 7 years in southern Quebec (Lamhamedi and Bernier 1994), from 8 to 15 years on a northern boreal forest site (~65° N lat.) (Hom and Oechel 1983), but up to 30 years in the subarctic (Chapin and Van Cleve 1981). Norway spruce needle longevity ranges from 6 to 7 years on a site in central Europe (51° N lat.) (Reich et al. 1996). Interestingly, Norway spruce had no genotypic predisposition toward longer-lived needles for sources from high latitudes or elevations (Reich et al. 1996). Numerous studies have found that increased needle longevity in conifer species occurs under limiting environmental conditions such as low seasonal temperatures, reduced solar radiation, reduced water, or nutrient availability (reviewed by Reich et al. 1992). This phenomenon of extended needle retention in conifers is hypothesized to be due to a simple cost–benefit scenario, with a balance between the cost of producing and maintaining needles in relation to the benefits of these needles having a positive photosynthetic capacity that continues over an extended period of many years (reviewed by Reich et al. 1992). Spruce species are able to maintain a high level of photosynthetic capacity over 4–5 years before rates gradually begin to decline (Section 2.2.3). Extended needle retention by spruce species enables them to maximize the net gain from a needle's ability to assimilate and allocate carbon over extended periods in relation to the initial investment of producing needles.

Shade shoots have a lower rate of needle packing (i.e., lower number of needles per stem unit length), and needles are usually developed at an angle close to a horizontal plane (Leverenz and Jarvis 1980; Carter and Smith 1985; Niinements and Kull 1995*b*; Germino and Smith 1999). This needle arrangement allows shade shoots to achieve near maximum P_n under nonsaturating light because of the horizontal needle arrangement and the small rate of interneedle shading along the shoot (Leverenz and Jarvis 1980). Needles on shade shoots are longer, narrower, and have a greater specific area (i.e., the needle surface area (cm^2) per gram of needle tissue) than needles grown on sun shoots (Krueger and Ruth 1969; Niinements and Kull 1995*a*; Man and Lieffers 1997; Chen 1997; Reich et al. 1998) (Fig. 2.6.1.3*a*). This needle development characteristic is how shade shoots occupy space to capture more sunlight under low light.

Sun shoots have a greater needle packing (i.e., higher number of needles per stem length), with most of the needles developed on the upper portion of the branch (Leverenz and Jarvis 1980; Carter and Smith 1985; Niinements and Kull 1995*b*). This needle arrangement does not affect overall shoot P_n. This is because open field conditions provide sufficient diffuse and reflected sunlight for all needles along the shoots, and this minimizes any influence of mutual shading and orientation on light interception (Carter and Smith 1985).

Spruce needle temperatures are influenced by the arrangement of needles along a branch. As was previously discussed, some of the solar energy that reaches the needle surface is absorbed (Section 1.1.3), while absorbed infrared irradiation also comes into the leaf from the surrounding environment (Section 1.1.1). Of the solar energy that is absorbed by spruce needles, a portion is lost as heat in the form of sensible heat, thermal radiation, and heat loss accompanying water evaporation. A small portion of the energy is also used in photosynthesis or other metabolism. The remainder is stored, thereby causing a change in leaf

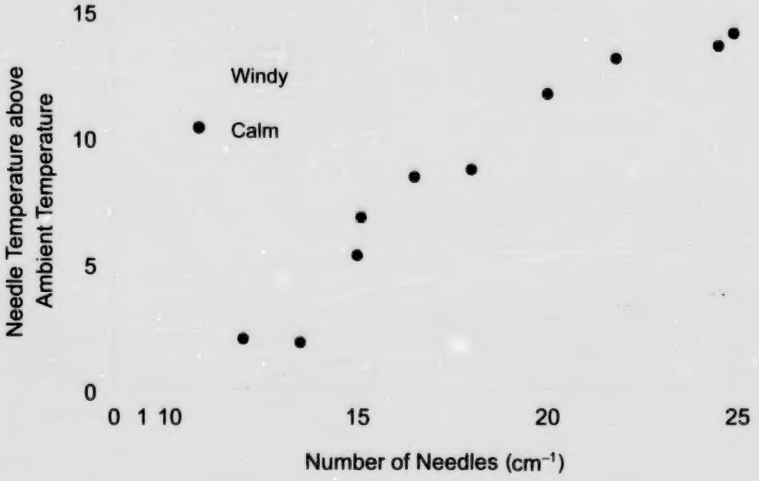
Fig. 2.6.1.3*a*. Specific needle area of Norway spruce in relation to their exposure to open sky (adapted from Stenberg et al. 1999). Canopy openness is defined as the unweighted fraction of unobscured sky.



temperature. In general, the temperatures of small leaves tend to be closer to ambient air temperature than the temperatures of larger leaves (Nobel 1991). This is because the dimensions of spruce needles allow for more effective convective exchange of energy between the leaf surface and the air. When needles are well spaced along the shoot, needle temperatures of conifers seldom differ from air temperatures by more than 0.5°C (Jarvis et al. 1976). However, a different needle temperature regime is found when the needles become tightly packed along the shoot system. When the number of needles within a centimeter of stem length increases, above 12 needles cm^{-1} of stem length, there is an increase in needle temperature above ambient air temperatures (Fig. 2.6.1.3*b*). This relationship still holds true under windy conditions, although the convective transfer of heat from the needles somewhat mitigates this phenomenon. Needle packing can cause needle temperatures to rise above ambient air temperatures.

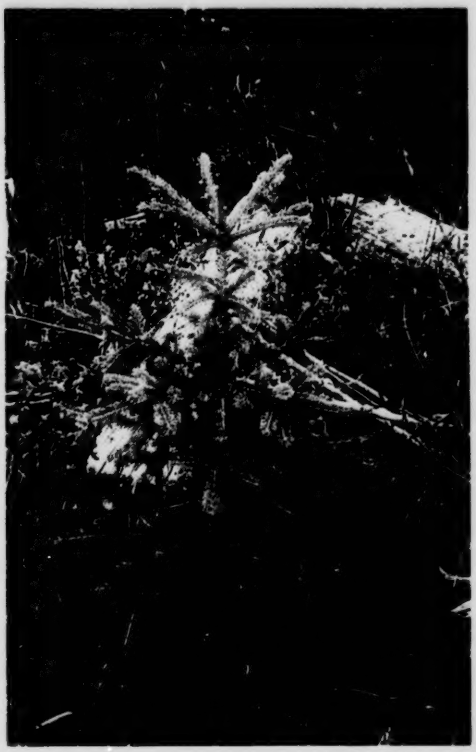
The phenomenon of needle packing may also have an effect on the photosynthetic process of spruce shoots. Spruce species inhabit forest environments where daily air temperatures during the summer growing season (Section 1.2.1) can be below the optimum levels required for maximum P_n (Section 3.3.1). Smith and Carter (1988) theorized that an increase in needle temperatures, resulting from needle packing, would result in increased P_n, because needle temperatures would be closer to the optimum temperature for maximum P_n. They estimated that needle packing along sun shoots can provide increased needle temperatures that would allow for 21–36% greater daily P_n than if needle temperatures were close to ambient air temperatures. These elevated needle temperatures for sun shoots may lead to substantial increases in seasonal P_n for spruce species that grow in regions having cold growing season conditions.

Fig. 2.6.1.3*b*. The temperature of Engelmann spruce needles above ambient air temperature in relation to the number of needles per centimeter of stem length under simulated full-sun (adapted from Smith and Carter 1988). Calm and windy conditions refer to wind flows of ~30 cm s^{-1} and ~3.0 m s^{-1}, respectively.



The architecture of the shoot system in spruce species is well defined and normally follows a symmetrical pattern. First-order branches that develop out of the bottom of the leader after each year's growth tend to be longer than branches formed down along the main stem (Fig. 2.6.1.3*c*). This results in a top-whorl of dominant branches followed by smaller interwhorl branches (Baxter and Cannell 1978; Cochrane and Ford 1978). Also, the main leader above the top-whorl does not form any first-order branches during the year of elongation, although buds form along the main leader and define locations of first-order lateral branch development during the subsequent growing season. These interwhorl, first-order lateral branches tend to be evenly distributed around the stem so that branches normally form in all spatial directions (Cochrane and Ford 1978). The number of these interwhorl lateral branches found along the main stem is influenced by the size of the parent structure. In other words, a bigger leader results in a greater number of lateral branches (Cannell 1974). This spatial distribution of first-order lateral branches for spruce species is important because it allows for an efficiently structured needle canopy. Cannell and Bowler (1978) suggested that this shoot form for spruce ensured minimal mutual shading of branches (i.e., low within-plant competition for light that can limit P_n, Section 3.1), even utilization of the vascular pathway of the stem, and even weight distribution of all branches on the stem. It must be recognized that the shoot architecture of first-order branches in relation to the leader is not based on a random distribution, but rather is a means by which lateral branches efficiently occupy the space around the stem.

Fig. 2.6.1.3c. Shoot system of a 4-year-old interior spruce seedling growing on a reforestation site in central British Columbia (photograph provided by R. Folk).



2.6.1.4 *Needle color*

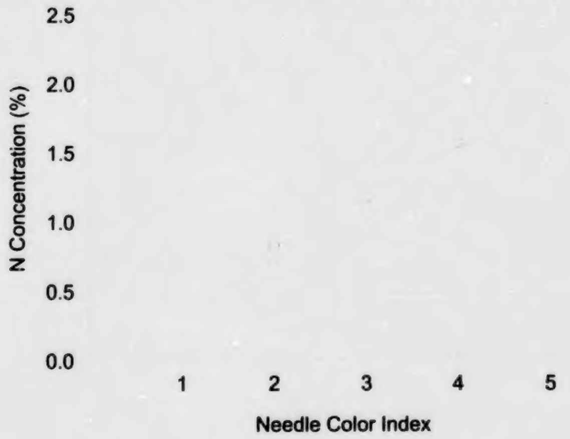
The color of spruce needles is related to chlorophyll and carotenoid pigments that are concentrated in the chloroplasts of needle mesophyll cells. Chlorophyll pigments are the light-absorbing pigments in the photosynthetic process. Chlorophyll pigments are green because they do not effectively absorb green wavelengths, rather they reflect or transmit these wavelengths (Section 2.2.3). Carotenoids are involved in the light-trapping process of photosynthesis, protect the chlorophyll from damage through photooxidation (Section 2.2.3), and can be a number of colors (i.e., red, orange, and yellow). Norway spruce seedling photosynthetic process is directly related to needle chlorophyll content under controlled conditions (Keller and Wehrmann 1963), although above a certain level, chlorophyll content is not always of primary importance in controlling photosynthesis under field conditions (Kozlowski and Pallardy 1996).

The color of spruce needles can range over an array of green shades. A number of conditions have been documented to explain this change in color. Changes in needle color that are seen in spruce seedlings in the field can be due to any one or a combination of these conditions.

First, needle chlorosis (yellowing) can occur if seedlings are deficient in certain nutrients that are critical to chlorophyll synthesis (e.g., N, Mg, Fe, Mn) or that affect nitrogen metabolism (e.g., Mo) (Section 2.3.3). Norway spruce suffering from either N, Mg, or K deficiency have needle yellowing and ~50% lower chlorophyll pigment concentration, compared to trees with green needles (Solberg et al. 1998). Also, the process of nutrient translocation that takes place in spruce species under limited site nutrient availability sometimes leads to chlorosis of the needles due to N deficiency (Section 3.6.1). The needle color of Norway spruce seedlings planted in a clear-cut is directly related to the N concentration; with a greater N concentration found in needles with a darker green color (Fig. 2.6.1.4). Increasing N concentration results in greater chlorophyll and carotenoid concentrations in Sitka spruce (Chandler and Dale 1995), while lower N concentration results in Norway spruce needles having a general bleaching of normal color due to a slight turn from chlorophyll (green) pigments towards lutein (yellow) pigments (Solberg et al. 1998).

Second, needle chlorosis can occur when seedlings are exposed to full sunlight. Open reforestation sites have been reported to contain higher percentages of chlorotic spruce seedlings than sites under a forest canopy (Tanner et al. 1996). Sitka spruce shoots that are exposed to full sunlight have lower chlorophyll contents than shoots growing in the shade (Lewandowska and Jarvis 1977). Norway spruce saplings that were released from competition had a reduction in chlorophyll content in fully developed needles (Gnojek 1992). This might be due to the fact that shade shoots need to invest in light-harvesting pigment to ensure efficient capture of available sunlight. In addition, needles of spruce seedlings are susceptible to solarization at high light levels. These high light intensities cause a destruction of chlorophyll, resulting in the yellowing of needles (Section 3.1).

Fig. 2.6.1.4. Changes in nitrogen concentration in relation to color of Norway spruce needles for seedlings planted on a boreal reforestation site in southern Sweden. Needle color index ranges from (1) yellow–green, (2) light green – yellow, (3) dark green – yellow, (4) light green, to (5) green (adapted from Bergquist and Örlander 1998).



Third, spruce needles can turn yellow as a result of freezing damage to the photosynthetic system of needles. This occurs on field sites where high light intensities can cause the phenomenon of cold-induced photoinhibition (Sections 3.3.1 and 3.7.4).

Fourth, water deficits can cause chlorosis in spruce needles. The chlorophyll content in Sitka spruce needles was reduced when seedlings were exposed to low water potentials (Beadle and Jarvis 1977).

Fifth, spruce needles tend to be more chlorotic during the winter compared to the summer. This seasonal change in spruce needle color is related to changes in pigment content. Spruce needles change their ratio of chlorophyll to carotenoids, with chlorophyll at a maximum from late spring to early fall, with chlorophyll content declining, and carotenoids are then at a maximum during the winter (Linder 1972; Lewandowska and Jarvis 1977; Köstner et al. 1990).

Sixth, spruce needle color changes as needles age. The chlorophyll content of Norway spruce needles is lowest in current-year needles and increases up to 4 years of age, although smaller differences occur between 2- and 4-year-old needles than between 1- and 2-year-old needles (Köstner et al. 1990).

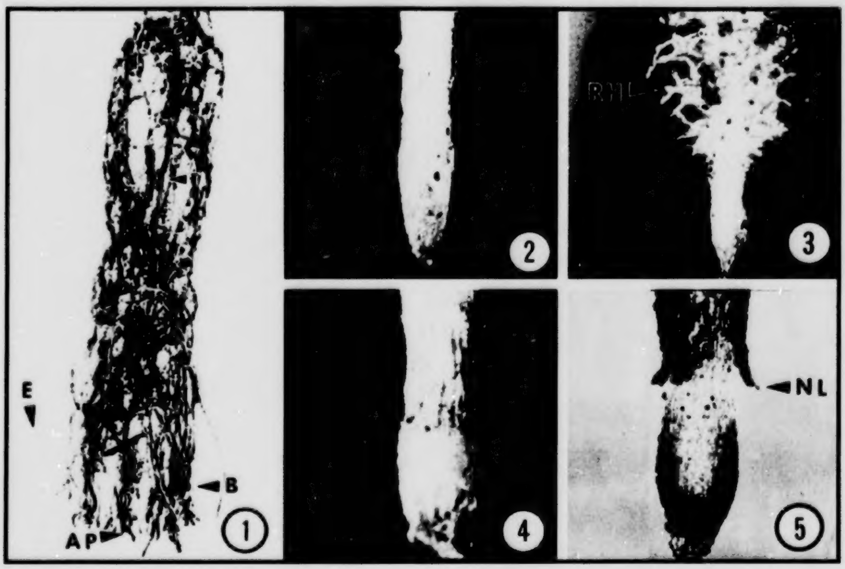
2.6.2 Root development

2.6.2.1 Root growth

The root apex, or tip, is the primary location of root growth, although in certain instances there can be an initiation and extension of new root meristem (Esau 1965). These regions give rise to all primary tissues of the new white root and also to production of the root cap. Root growth is confined to a small region (2–3 mm) just behind the root apex, with lateral roots occurring some distance behind the root apex (Salisbury and Ross 1992). When a new lateral root emerges from the parent root, it has an organized apical meristem and a root cap. These new lateral roots then elongate and form different types of roots within the overall root system.

Long, lateral roots of white spruce seedlings can be divided into three categories based on external morphology (Johnson-Flanagan and Owens 1985*a*) (Fig. 2.6.2.1*a*). First, elongating roots are white and devoid of root hairs. Second, absorbing, or lateral roots have root hairs that are proximal to the zone of elongation and are usually 3 cm in length. These lateral roots anchor the root system to soil particles, dramatically increasing the total area of the root system. These roots are the primary location through which the root system absorbs water (Fig. 2.1.2*b*) and minerals (Fig. 2.3.1). Third, when root elongation ceases, roots turn brown due to suberization of the endodermis and metacutization (i.e., suberin is laid down on the cell walls as a suberin layer) of a discrete layer surrounding the root apex (Fig. 2.6.2.1*a*). Renewed growth is marked by swelling of the brown root apex and the emergence of a white root tip. Interestingly, during seasonal periods of maximum root growth (see next paragraph), both elongating and absorbing roots can grow (Johnson-Flanagan and Owens 1985*a*). However, during other times of the year, there is variation in root growth within these root classes, indicating nonuniform seasonal development patterns.

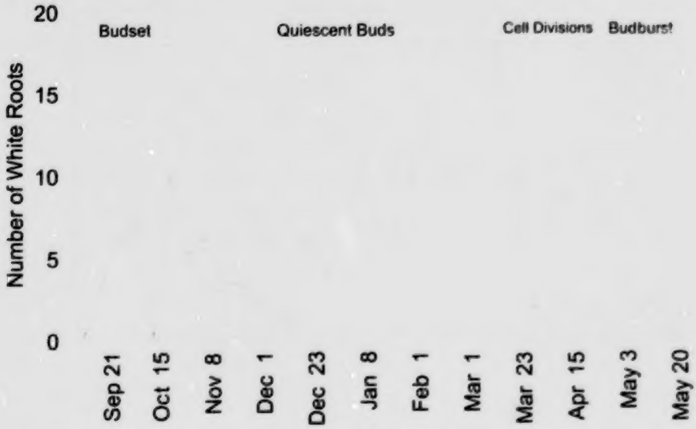
Fig. 2.6.2.1*a*. Root morphology for container-grown white spruce seedlings: (1) container-grown seedling root system (E, elongating root; B, brown root; AP, air-pruned roots); (2) elongating root; (3) absorbing root with root hairs (RH); (4) brown root; (5) newly elongated root emerging from necrotic layer (NL) (from Johnson-Flanagan and Owens 1985*a*).



Seasonal periodicity of root growth has been attributed to the annual dormancy cycle. In spruce species, this seasonal periodicity in root growth causes peaks to usually occur in early spring and early fall (Fig. 2.6.2.1*b*). Numerous studies have found a relationship between conifer seedling root growth capability and fall shoot dormancy patterns; root growth decreases as shoot dormancy intensifies in late fall and early winter (Ritchie and Dunlap 1980). As conifer species move from a dormant to a quiescent phase, there is then an increase in root growth. This pattern is known to occur in Engelmann (Burr et al. 1989), white (Johnson-Flanagan and Owens 1985*b*), and Sitka (Deans and Ford 1986; Coutts and Nicoll 1990) spruce seedlings. Norway spruce trees had a peak in root growth in early summer, after shoot growth was completed, and then another peak in root growth in late summer, prior to a decline in the fall (Lyr and Hoffmann 1967).

Root growth diminishes just prior to and after budbreak, when shoot growth activity occurs, in the spring (Johnson-Flanagan and Owens 1985*b*; Deans and Ford 1986). The spring reduction in root growth has been attributed to the preferential access of the actively growing shoot to photosynthates produced during photosynthesis (Kramer and Kozlowski 1979) (Section 2.2.3). Actively growing spruce roots have a 38% depletion in their total storage carbohydrate level when compared to suberized inactive roots (Johnson-Flanagan and Owens 1985*b*).

Fig. 2.6.2.1*b*. Seasonal pattern of root growth (measured as the mean number of white roots from one main lateral of four seedlings) for white spruce seedlings in relation to bud development (indicated by arrows) and time of year (adapted from Johnson-Flanagan and Owens 1985*b*).



Spruce species have a seasonal variation in their root respiration rates, with a strong relationship occurring between root elongation and increased levels of root respiration (Lahde 1967; Johnson-Flanagan and Owens 1986). The need for additional photosynthates required for continued root growth does exist when shoot growth is occurring. In addition, the spring reduction in root growth has also been attributed to changes in the hormonal balance (Ross et al. 1983). This spring and summer seasonal pattern of diminished conifer seedling root growth occurs when active shoot growth is occurring (Ritchie and Tanaka 1990).

There is a widely held belief that new root growth, which requires photosynthates, utilizes currently produced photosynthates rather than carbohydrate reserves (Ritchie and Dunlap 1980). As stated above, it is believed that the spring reduction in root growth is partially attributed to the preferential access of the shoot to photosynthates. That is, the new developing shoots are a stronger sink for photosynthates than the developing root system. Evidence supporting this hypothesis for spruce species is unclear. There is conflicting evidence showing initial new root growth in spruce being supported by currently produced photosynthate, with some work supporting van den Driessche (1987), while other work is discounting (Philipson 1988; Thompson and Puttonen 1992) this hypothesis. However, only limited root growth takes place in continuous darkness, with further root growth beyond an initial period (~7–10 days), requiring currently produced photosynthate, or root growth declines rapidly (Philipson 1988, Binder et al. 1990). Environmental factors that affect the acquisition of photosynthates can subsequently alter spruce seedling root growth patterns.

It must be recognized that even though spruce species have a seasonal root growth pattern, field site environmental conditions influence the actual development pattern. Root growth declines with decreasing soil temperature (Section

3.5.1) and water potential (Section 3.5.2.1), or when soil becomes saturated (Section 3.5.2.2). Norway spruce tree did not have a peak in root growth prior to budbreak in the spring, and this was attributed to low soil temperatures (Lyr and Hoffmann 1967). Root growth of plantation-grown Sitka spruce was found to increase when soil water or temperature increased during the growing season (Deans 1979). Any discussion of inherent seasonal root growth patterns for spruce species must be considered in light of the effects that edaphic conditions at the field site have on root growth.

2.6.2.2 Root system form

Extensively branched root systems are important for the effective extraction of water and mineral nutrients from the soil. Root systems of forest trees develop in response to complex genetic, physiological, and atmospheric environmental interactions, subject to limitations imposed by aboveground growth and limiting levels of edaphic factors (Sutton 1969, 1980, 1991). In general, root concentration decreases rapidly with soil depth, thus root form is directly related to site edaphic conditions.

Spruce species have shallow to deep root systems, with the extent of root penetration dependent upon the soil properties (Wagg 1967; Sutton 1969; Eis 1978). The actual amount of root growth and subsequent root system form depends upon the physiological response of a spruce seedling to edaphic conditions. The spruce seedling response to the edaphic conditions of water content, temperature, oxygen content, and fertility affects the subsequent form of the root system. Section 3 provides examples of the impact of edaphic conditions on the root growth of spruce seedlings. Unlike the organized development of the shoot system, which occurs aboveground, the soil structure itself creates mechanical impedance to the development and form of the root system (Sutton 1969). This impedance is due to the mechanical composition or the solid phase of the soil. The solid phase is made up of soil particles, whose size and shape have a direct influence on the soil texture (i.e., sand, silt, and clay), or the density, pore size, and rigidity of the soil.

Due to the nature of the soil system (i.e., the combination of soil environment and soil structure), the root system form in spruce species takes on many shapes. For example, in soils that are well drained and have a uniform texture, young spruce trees can develop a taproot (Sutton 1969; Eis 1978; Schultz 1978). In other boreal forest locations, young and mature spruce trees have a preponderance of root systems in the upper portions of the soil profile due to well-developed organic soil horizons (Eis 1970; Kimmins and Hawkes 1978; Strong and La Roi 1983), high water tables (Fraser and Gardiner 1967; Finer 1989), optimum soil water availability (Deans 1979), or cold soils (Tyron and Chapin 1983; Van Cleve et al. 1983; Steele et al. 1997). The depth and extent of root development with spruce species appears to have considerable plasticity that is adaptable to the soil environment.

Spruce species develop root systems under a dynamic process. This occurs because there is variation in the longevity of roots to be retained as part of the root system. When conditions for growth are optimal, spruce species can rapidly develop long lateral roots out into the surrounding soil (reviewed by Sutton 1969). Within a week or so after formation, these lateral roots can turn brown, or become suberized, which enables these roots to be retained for a period that can extend over many years. This root suberization prevents the possibility of root desiccation, although it also decreases the permeability of roots to water (Section 2.1.2). Lateral roots continue to develop and can become a long-term component of an established seedling root system. However, if deleterious edaphic conditions occur, these long lateral roots die.

A unique feature that contributes to the root system form of spruce species is that root systems are a dynamic system with a rapid turnover of short-lived, short, and fine roots during the growing season. Short roots develop off of long lateral roots and can persist for time periods of greater than 1 year (Sutton 1969). There is a wide range in variability in short-root retention, depending upon whether roots develop into woody roots that are suberized and contain secondary xylem. In black spruce stands, fine dead roots (<5 mm in diameter) comprised ~25% of the total fine-root biomass found within the soil profile (Steele et al. 1997), indicating a rapid turnover rate on a yearly basis. In Sitka spruce seedlings, 95% of fine roots survived for at least 14 days, although only 53% of fine roots survived for at least 63 days (Black et al. 1998). This turnover of fine roots has been attributed to seasonal changes in edaphic conditions such as soil water (Deans 1979) and soil temperature (Lawrence and Oechel 1983; Hendrick and Pregitzer 1993). As a result, root systems typically use one half or more of the photosynthates produced by a plant (Kozlowski et al. 1991). Root growth, as well as maintenance respiration, are the major diversions of photosynthates from shoot system development. The short-lived nature of these fine roots is probably driven, in part, because of their high maintenance respiration costs as well as their susceptibility to limiting site edaphic conditions.

Conifer species, in general, have a greater development of a coarse fine root system compared to deciduous tree species and the understory vegetation. Both white spruce (Bauhus and Messier 1999) and Norway spruce (Clemensson-Lindell and Persson 1995) have low specific root lengths (i.e., total root length divided by root mass), which indicates that spruce species develop thicker and longer-lived roots that exploit less of the soil system. Bauhus and Messier (1999) speculated that this conservative root development strategy may be an adaptation to conditions where root growth is normally limited in the low-resource environment of climax northern latitude forests. In contrast, deciduous tree species (Fahey and Hughes 1994; Bauhus and Messier 1999) and the understory vegetation (Bauhus and Messier 1999) within the northern latitude forests have high specific root lengths which allow these species to maintain a highly ramified thin fine root system to maximize the exploitation of the soil system. One of the ways that competing vegetation gains dominance over tree seedlings in a disturbed habitat is to produce a root system which causes an expanding zone of depletion for water and nutrients down through the soil profile (Grime 1979). Differences in root system development between spruce species and deciduous vegetation is probably one the reasons why competing vegetation can limit the performance of spruce seedlings on reforestation sites (e.g., Section 5.5.3: Soil water and Section 5.5.4: Fertility).

Site preparation treatments that alter site edaphic conditions (Section 5.5), in turn, alter the planted seedling root system form. Site preparation treatments that increase soil temperatures can enhance root development (Balisky and Burton 1997). For example, spruce seedlings planted in mounds on wet planting sites have more extensive root development than those planted in low spots (von der Gönna 1989, Coutts et al. 1990). This greater root development in spruce seedlings planted on mounds is maintained for many years. White spruce seedlings that had grown for 12 years on mounded planting sites had 2.5 times more roots that were also thicker (i.e., 5 times the aggregate cross-sectional area) than seedlings planted in untreated ground (Heineman et al. 1999). In addition, root growth beyond the mound, as well as the depth and location in the soil substrate of main lateral roots, was similar to seedlings planted in untreated ground. Heineman and associates (1999) felt that the long-term mechanical stability of white spruce seedlings planted on mounds would be similar to that of seedlings planted without site preparation. Foresters must recognize that the proper selection or creation of planting spots is necessary to ensure seedlings have the microsites best suited to provide edaphic conditions that allow extensive root development.

The form of a container-grown spruce seedling root system is initially dictated by the media-plug and cavity size. Container sidewalls limit the horizontal root extension, and primary laterals grow downward with air-pruning of these roots at the bottom of the container cavity (Fig. 2.6.2.1*a*). This creates a regular root form with extensive branching but few, short, lateral roots (Johnson-Flanagan and Owens 1985*a*). Due to the low number of primary lateral roots found in the upper portion of the container plug, initial root growth is dominated by roots that develop out of the bottom, rather than top, portion of the container plug (Fig. 2.6.2.2*a*). This container-grown root form influences subsequent root development patterns once seedlings are planted in the field.

Root architecture of container-grown seedlings differs greatly from that of root systems formed naturally in the field (Burdett 1990; Halter et al. 1993). Interior spruce seedlings can develop roots outward from all areas of the container plug over the first field season, although the preponderance of root development occurs from the bottom portion of the container plug (Fig. 2.6.2.2*b*). Due to the initial container plug root form, there are a greater number of longer roots developing out of the lower half of the root plug. This pattern of greater root development out of the bottom portion of the container plug during the initial establishment phase is typical of container-grown spruce seedlings (e.g., Grossnickle and Reid 1983; Grossnickle and Major 1994*b*; Krasowski et al. 1996; Balisky and Burton 1997), and may be a concern on sites where low soil temperatures (Section 3.5.1) or excessive soil water (Section 3.5.2.2) limit the

Fig. 2.6.2.2*a*. Root growth for container-grown interior spruce seedlings ($N = 24$: mean + SE) partitioned into the upper and lower half of the container plug (S. Grossnickle and R. Folk, unreported data).

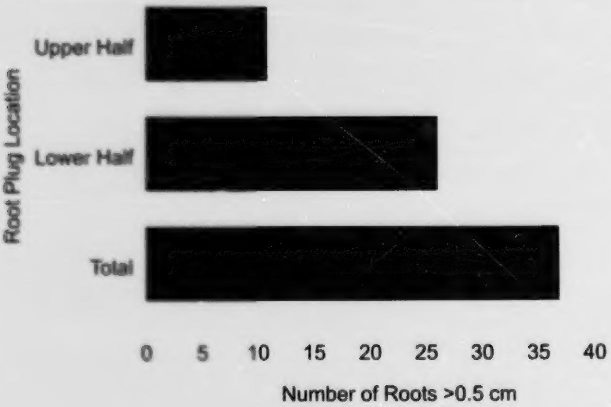
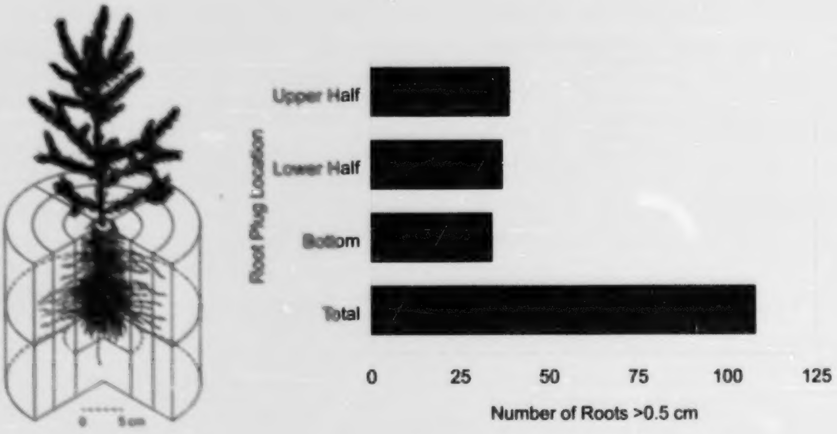


Fig. 2.6.2.2*b*. Root development (mean + SE) for container-grown interior spruce seedlings after one growing season on a reforestation site (adapted from Grossnickle and Major 1994*b*).



root growth of spruce seedlings. The amount of initial root development shown in Fig. 2.6.2.2*b* is typical of spruce seedlings grown under good edaphic conditions during the first growing season in the field (Sutton 1969; Nienstaedt and Zasada 1990). By the end of the second growing season, white spruce seedlings can develop roots that are up to 100 cm in length and grow to a depth of 50 cm under optimum edaphic conditions (Sutton 1969; Burdett et al. 1984).

The root system of a container-grown spruce seedling continues to develop, following a pattern of the original root form produced within the container system and the species response to the reforestation site edaphic and soil texture conditions. For example, 5 years after planting, container-grown Engelmann spruce seedlings on an afforestation site showed a greater portion of roots growing out of the lower half of the plug in mineral soil; this root form was even more prevalent when seedlings were grown in a soil having a surface organic layer that dried out on a regular basis (Grossnickle and Reid 1983). Sitka spruce grown as containerized seedlings had a portion of their root development occurring in a horizontal pattern in the upper portion of the soil profile, although they had greater root development out of the lower portion of the original container root plug, 5–6 years after being planted on a range of reforestation sites (Carlson et al. 1980). In contrast, when black spruce container-grown seedlings were planted in soils with high levels of sand, silt, or loam, root development 5 years after planting was predominantly in the upper portions of the soil profile, with very few deep or vertical roots (Girouard 1995). This form was attributed to the container growing process that air-pruned the taproot and any primary laterals. The deep planting of container-grown black spruce seedlings also encouraged the development of adventitious roots on the lower portion of the stem (Girouard 1995). In these examples, the combination of the initial root form of container-grown spruce seedlings and edaphic and soil texture conditions on the site influenced root development patterns during seedling establishment and transition phases on reforestation sites.

Persistence of the container-grown root system form, well into the early stages of plantation development, has created a concern of how this modified root form affects long-term plantation success. The lack of a natural root form and root distribution may result in reduced mechanical stability, altered nutrient and water relations, and reduced growth potential of planted conifer seedlings (Nichols and Alm 1983; Halter et al. 1993; Balisky et al. 1995). Although planted spruce seedlings had differences in root form when compared to natural seedlings, the container-developed root system morphology did not appear to limit growth or cause instability after 5–6 years in the field (Carlson et al. 1980; Girouard 1995). After 15 years in the field, these initial differences in root form appeared to be minor (Scagel and Evans 1992). The ability of spruce species to produce adventitious roots has long been felt to be a reason why container-grown seedlings can overcome the imprint of this nursery cultural practice (Van Eerden 1982). The length of time and degree of effect of container nursery culture practices on root development of spruce seedlings is still open for debate. Further examination of the influence of this practice on root form and development is required.

3 Ecophysiological response

Each forest species has its own unique pattern of physiological response to field site environmental conditions. In this section, the physiological performance of northern latitude spruce species in relation to environmental conditions is examined. It must be recognized that environmental conditions change daily, seasonally, and yearly. Spruce species show physiological responses to these changing environmental conditions. This physiological performance of spruce in response to the environment ultimately determines the seedling's subsequent growth performance in relation to field site conditions.

In Sections 3.1 through 3.5, the discussion centers around the gas exchange processes of spruce species in relation to atmospheric (i.e., light, humidity, temperature, and wind) and edaphic (i.e., soil temperature and water) conditions that occur in the field. Where available, information on spruce seedling growth is discussed in relation to these conditions. Section 3.6 examines the physiological performance and morphological development of spruce species in relation to mineral nutrition. This discussion on mineral nutrition specifically examines spruce species response in relation to nitrogen (N) and phosphorus (P) levels. Section 3.7 discusses the seasonal patterns of freezing tolerance and dormancy of spruce species. Section 3.8 presents examples of seedling performance in relation to combinations of environmental factors that can occur on a field site. The final section (Section 3.9) provides the reader with some insight into the dynamic nature of physiological response and morphological development that occurs for spruce seedlings in a yearly cycle.

This section is intended to provide the reader with examples of spruce species physiological response to potential field site environmental conditions and the effect of these responses on subsequent growth. This is the background information necessary for understanding the performance of spruce seedlings planted on reforestation sites.

3.1 Light

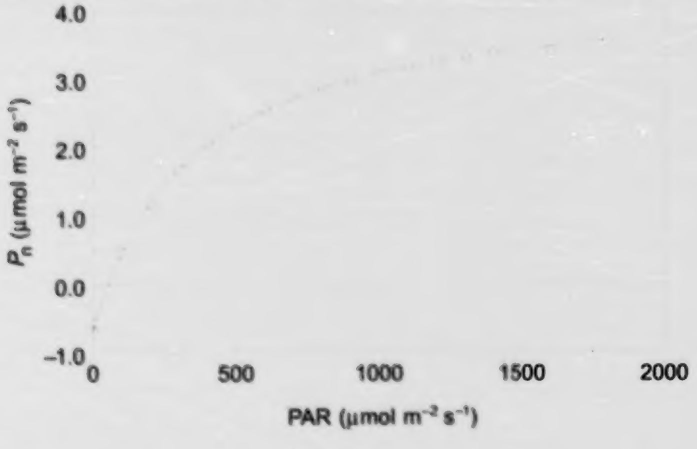
Seedlings usually receive full sunlight just after planting on a clear-cut reforestation site. When seedlings reach the transition phase of the forest regeneration process (Section 5.5.1), or when seedlings are grown under a partial forest canopy retention system (Section 5.6), competing vegetation alters light received by the seedlings. This dynamic pattern of competing vegetation development changes light received by spruce seedlings and affects gas exchange processes and subsequent growth on northern forest reforestation sites.

Stomata of spruce respond to increases in light intensity in two phases (Kaufmann 1982*a*; Watts et al. 1976; Goldstein et al. 1985; Grossnickle and Blake 1986). First, there is a rapid opening of stomata from 0 to 10% full sunlight. Second, stomata continue to gradually open from 10% to full sunlight. Stomata on Sitka spruce needles can achieve two-thirds of maximum stomatal opening after a 40-min adjustment to light following a dark period, although complete stomatal adjustment can take up to 4 h (Watts and Neilson 1978).

Net photosynthesis (P_n) shows a similar two-phase response to light. During the first phase, P_n is below the light compensation point at <5% full sunlight. In spruce, the dark results in no photosynthesis, so the CO_2 produced in respiration is released from leaves. As light intensity increases from dark conditions, a point is reached where the photosynthetic uptake of CO_2 equals its release due to respiration. This is called the light compensation point, and at this point, there is no net CO_2 exchange occurring between the leaves and the atmosphere. The light compensation point varies because of many factors: species, needle type, needle age, CO_2 concentration in the air, and air temperature. In spruce species, P_n rises rapidly up to 25–33% full sunlight and then increases only gradually after that point (Fig. 3.1*a*). Spruce species reach light saturation of photosynthetic processes between 25 and 50% full sunlight (Krueger and Ruth 1969; Ronco 1970; Ludlow and Jarvis 1971; Watts et al. 1976; Grossnickle and Major 1994*b*; Fan et al. 1997). Thereafter, increasing light results in only a slight increase in P_n. Needle distribution around the twigs of shoot systems of spruce species can cause P_n not to reach complete light saturation of all foliage because of mutual shading of the needles. Leverenz and Jarvis (1979) found that maximum photosynthetic capacity of a Sitka spruce branch is not reached until every foliage photosynthetic unit is saturated. This is possibly why there is still a gradual increase in P_n at light that is normally considered above the light saturation level for spruce.

In the above discussion, the gas exchange response of spruce species to light has been presented independent of changes in vapor pressure deficit (VPD). Under field conditions, both light and VPD continually change in an interrelated fashion (Section 1.3.2). High light levels are sometimes accompanied by high VPD, although there regularly are times during the growing season when high light levels do occur at low VPD. A discussion of P_n response to multiple environmental variables is presented later in this treatise (Section 3.8).

Fig. 3.1*a*. The pattern of net photosynthesis (P_n) for interior spruce seedlings over a range of photosynthetically active radiation (PAR) (adapted from Fan et al. 1997).

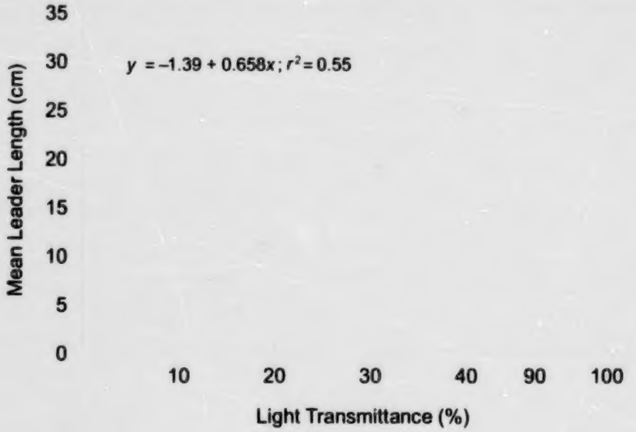


Conifer species P_n responds very rapidly to changes in light intensity, due to either clouds or partial shading from overstory canopy (i.e., sun flecks, Section 1.1.2), while needle conductance (g_{wv}) responds more slowly or not at all to these changes in light (Knapp and Smith 1989, 1990; Pearcy 1990). Since stomata remain open during both sun and shade periods of the day, under optimum soil water, conifer species have a positive carbon gain through the rapid increase in P_n as light becomes available. This strategy allows for greater carbon gain, although greater water loss, in response to variable sunlight. As a consequence, conifer species, such as spruce, have lower WUE under variable sunlight.

Low light levels can affect the survival of spruce species. Low light does not affect the survival of spruce seedlings over at least the first 3 years after being field-planted (Chen 1997). However, white spruce trees slowly die when they are exposed to light at less than 15% full sunlight in the understory for many years (Eis 1970). These low light intensities that can cause mortality are just above the compensation point for P_n of spruce species.

Spruce seedling shoot development is influenced by light within the growing environment. The seasonal rate of shoot growth increases rapidly between 15 and 40% full sunlight, with shoot growth at 40% full sunlight comparable to full sunlight (Gustafson 1943; Shirley 1945; Logan 1969) (Fig. 3.1*b*). Shoot growth requires light intensities above 20%, with maximum shoot growth occurring at 60% full sunlight (Jobidon 1994). White spruce seedlings grown for 8 years in 50 and 75% full sunlight had similar height growth; seedlings grown in the same experiment at 25% full sunlight showed much less height growth (Gustafson 1943). Eis (1967) found that height growth of white spruce at 60% full sunlight

Fig. 3.1*b*. Average leader length (over the two previous growing seasons) of white spruce saplings in relation to overstory light transmission (adapted from Lieffers and Stadt 1994). Light transmission was calculated as light below the canopy / light above the canopy.

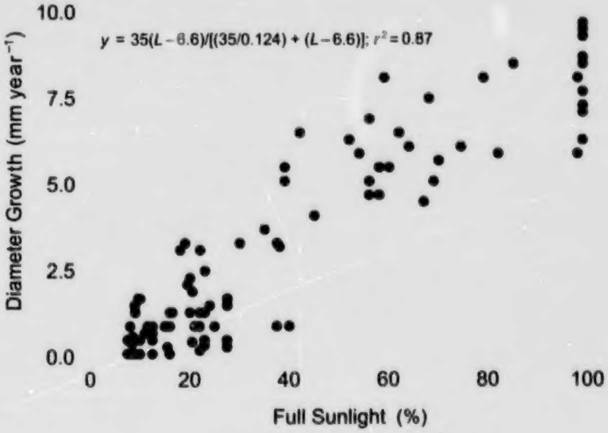


was twice that of seedlings under 20% sunlight. Diameter growth also increases with greater light intensity (Fig. 3.1*c*). Several studies also demonstrate that diameter growth of white spruce seedlings is affected by light intensity more than height growth, with increased light resulting in increased diameter growth (Shirley 1945; Eis 1967; Logan 1969; Brix 1972). Other work found both height and diameter (Chen 1997; Coates and Burton 1999) and volume (Comeau et al. 1993) growth increase with greater light. These studies show different shoot growth response to light intensity. This is probably due to the discrepancy in tree age of sample populations. As seedlings grow into trees, changes in crown architecture occur, such as increased needle density and age, within-crown differences in needle structure and orientation, and self-shading of branches (Section 2.6.1.3). These differences in shoot system form affect the whole-plant growth response of developing young trees to incoming light.

Root growth of spruce species is also affected by light intensity. Reduced light causes a decrease in root development of spruce seedlings (Jäderlund et al. 1997; Reich et al. 1998). Reduced light intensity can cause carbohydrate deficiency throughout the plant, thereby limiting the allocation of carbohydrates to the root systems of seedlings (Björkman 1981). This occurs because of the relative strength of various sinks, and thus, the preferential translocation of photosynthates is to the shoot system (Section 2.2.3) when there are limited photosynthates within a spruce seedling. The conclusion to be drawn from all of this work is that light levels can alter both the above- and below-ground morphological development of spruce species.

The arrangement and structure of needles along the branches of spruce species change in relation to light intensity. Briefly, needles on shade shoots are

Fig. 3.1*c*. Diameter growth rates (average increment per year over 3, 4, and 5 years after field planting) of hybrid spruce seedlings in relation to percent of full sunlight on sites having a range overstory canopy structure (Hazelton, B.C., 55°22′ N, 127°50′ W) (adapted from Coates and Burton 1999).



characterized by lower needle packing, a more horizontal plane along the shoot, and a greater specific needle surface area than sun shoots (Section 2.6.1.3). These changes in needle arrangement and structure improve the ability of shade shoots to capture light for P_n under low light.

Photoinhibition typically occurs in plants that are grown in the shade and then suddenly exposed to high light intensities; this response is reported to be greater in shade tolerant plants (Kozlowski and Pallardy 1996). Photoinhibition is characterized by a reduction in a needle's quantum efficiency, that is, the amount of CO_2 fixed per absorbed quantum of light. This is due to an inactivation of the photochemical process of photosynthesis, causing a reduced absorption of light. Such a response has strong implications when a species such as spruce is suddenly exposed to high light intensities after applying various silvicultural practices (i.e., thinning, alternative silvicultural systems, or removal of vegetation competition). There are variable response patterns reported in the literature on the effects of long-term low light on the subsequent P_n of spruce species after release from an overstory canopy. Sitka spruce seedlings preconditioned in heavy shade had higher P_n at low light intensities (i.e., <10% full sunlight) and reached light saturation at lower light intensities than seedlings preconditioned in light shade (Krueger and Ruth 1969). Norway spruce saplings that were suppressed under a heavy hardwood canopy exhibited photosynthetic damage, following a release cutting, although they recovered their photosynthetic capacity by the following growing season (Gnojek 1992). Spruce needles grown under low light have greater chlorophyll content than needles grown under full sunlight (Section 2.6.1.4). These shade needles can undergo chlorosis, a loss of chlorophyll without a concomitant loss of carotenoids (which protect the chlorophyll), after exposure to higher light. In contrast, white spruce seedlings grown under low light of a hardwood canopy had rapid development of normal P_n after a release to full sunlight (Lieffers et al. 1993). Lieffers and associates (1993) attributed the rapid recovery of P_n in white spruce, in part, to the exposure of seedlings to intermittent high irradiance while under the hardwood canopy (i.e., high winter light, periodic insect defoliation of the canopy during the summer, higher light penetration through the canopy compared to a conifer overstory; Fig. 1.1.2*b*). This could have allowed the needles to develop attributes more characteristic of sun rather than shade needles. The influence of canopy structure on the rate of light penetration through the canopy to the spruce seedlings may affect the seedling photosynthetic capacity subsequent to an overstory release treatment.

Spruce seedlings are susceptible to solarization (i.e., yellowing of needles) at high light (Ronco 1970). Potentially damaging conditions also occur when either low temperatures (Section 3.3.1) or water stress occur simultaneously with excess light. Under conditions of stress, chloroplast pigment absorbs more light energy than can be used in photosynthesis. If the plant is unable to dissipate the excess energy through heat and (or) fluorescence emission, photodamage can result (Gillies and Vidaver 1990). In Engelmann spruce, this can cause destruction of the chlorophyll and result in a yellowing or "sunburning" of the needles (Ronco 1970, 1975). Engelmann spruce seedlings protected with partial shading are not affected by solarization (Ronco 1975). Also, as conifers become dormant and cold-hardened, mechanisms develop to protect chloroplasts from photodamage (Gillies and Vidaver 1990). These findings indicate that solarization of spruce needles is due to an exposure to high light in combination with other limiting environmental conditions and the phenological state of spruce seedlings during the exposure period.

The quality of light changes as it passes through the overstory canopy, with the red to far-red light ratio and blue light decreasing below vegetation cover (Section 1.1.2). Plants are also affected by the red to far-red light ratio, with light quality altering plant form and structure. In many plant species, a decrease in the red to far-red light ratio can trigger responses such as increased stem elongation, reduced leaf to stem dry weight ratios, increased shoot to root ratios, and reduced photosynthetic capacity (Smith 1982, 1994). However, how this red to far-red light ratio affects the morphological development of spruce species is not clear. In one study, when the red to far-red light ratio was increased, white and Engelmann spruce seedlings had greater height and diameter growth and an increased number of branches (Dymock and Wilson 1984). On the other hand, black and white spruce seedlings had no difference in height and diameter growth after being grown in either red or far-red light, although seedlings grown under red light had a lower shoot to root ratio due to enhanced partitioning to the roots (Hoddinott and Scott 1996*a*). Exposure of black and white spruce seedlings to long periods of either red or far-red light also had no effect on needle chlorophyll content or the light-harvesting activity of photosynthesis (Hoddinott and Scott 1996*b*). In addition, the level of blue light is also known to alter several photomorphogenic responses, including inhibition of shoot elongation (Smith 1994). Further work is needed to describe how the quality of light affects growth and allocation patterns for spruce species.

3.2 Humidity

Spruce seedlings are exposed to a wide range of atmospheric conditions on reforestation sites. This occurs because temperature and relative humidity of the air are continually changing, and they determine the evaporative demand of the atmosphere. Under these conditions, water evaporates from the liquid surface of the mesophyll cells inside the leaf stomata (Fig. 2.2.1*a*). A vapor pressure deficit (VPD) occurs because of the difference between the saturated water vapor pressure in leaf stomata, at a given temperature, and the vapor pressure of surrounding air (Section 1.3.2). The daily change in VPD on a reforestation site has a direct influence on the Ψ and g_{wv} of spruce seedlings, and long-term exposure to high VPD may affect seedling growth. In this way, the daily and growing season humidity patterns of the reforestation site can influence spruce seedling performance.

Under adequate soil water, stomata remain at least partially open during the day, and fluctuations in VPD cause changes in Ψ (Ritchie and Hinckley 1975). The daytime change in Ψ of spruce seedlings is typically driven by VPD influencing transpiration, when soil water is not limiting (Fig. 3.2*a*). This occurs because the loss of water from open stomata, in the form of water vapor, is controlled by the VPD gradient between water evaporating from needle surfaces within the stomata and the outside air. Water deficits (lower Ψ) increase because resistance limits water flow along the SPAC pathway to meet the evaporational demands placed upon the seedling shoot system (Section 2.1.2). This type of response between Ψ and VPD occurs in both white and black spruce (Grossnickle and Blake 1985) and Engelmann spruce (Grossnickle and Reid 1985) seedlings on reforestation sites having adequate soil water.

Stomata of spruce species are sensitive to daily changes in VPD. Interior spruce seedlings have high g_{wv} when evaporative demand is low (Fig. 3.2*b*). As VPD increases, there is a reduction in g_{wv}. The dramatic decrease in g_{wv} to increasing VPD is due, in part, to lower shoot Ψ. In addition, lower Ψ_{soil} can cause greater stomatal sensitivity (see below), thus lower g_{wv} at higher VPD (Pallardy et al. 1995). This pattern of decreasing g_{wv} with increasing VPD is typical of spruce species when measured under field conditions (e.g., black: Grossnickle and Blake 1986, 1987*b*, Dang et al. 1997; Engelmann: Kaufmann 1976, 1982*a*, Grossnickle and Reid 1985; interior: Grossnickle and Major 1994*b*; Sitka: Watts and Neilson 1978, Beadle et al. 1985*a*, 1985*b*; white: Goldstein et al. 1985, Grossnickle and Blake 1986, 1987*a*, 1987*b*).

Fig. 3.2*a*. Change in white spruce seedling shoot water potential (Ψ) in response to the vapor pressure deficit (VPD) at a reforestation site (adapted from Grossnickle and Blake 1986).

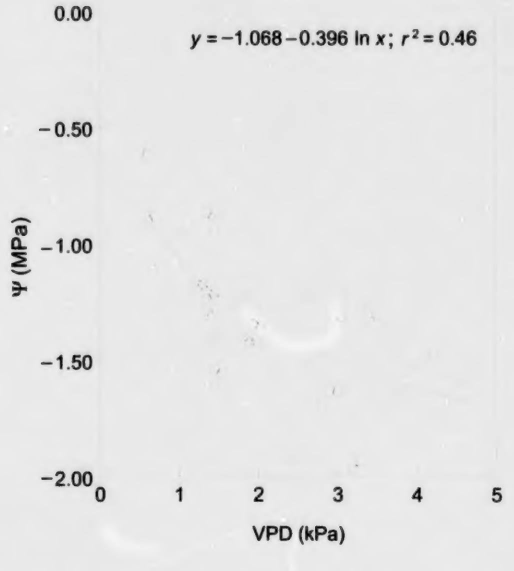
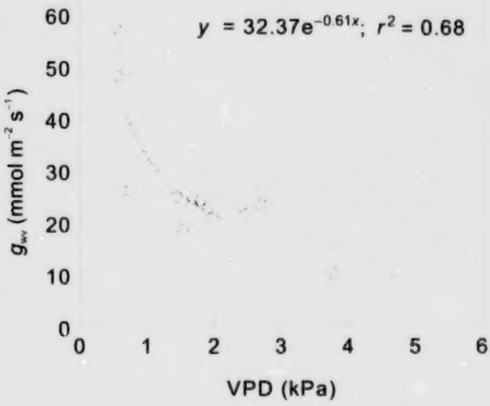


Fig. 3.2*b*. Needle conductance (g_{wv}) of interior spruce seedlings in response to a range of summertime vapor pressure deficit (VPD) on a boreal reforestation site (adapted from Grossnickle and Major 1994*b*).



Spruce species have a distinct pattern of g_{wv} response to daily plant water stress. There is a general decrease in g_{wv} as Ψ becomes more negative (Fig. 3.2*c*). This occurs during the day, even when there is available soil water, and is due to the interaction of seedling g_{wv} changing in response to both VPD and Ψ. Under optimum soil water, daytime fluctuations in VPD are reflected in seedling Ψ (Fig. 3.2*a*) and g_{wv} (Fig. 3.2*b*). This response has been defined as stomatal feedback control (Sheriff 1977; Schulze 1986). Under stomatal feedback control, daytime changes in g_{wv} are explained by stomatal response to changes in needle Ψ, which in turn are dependent upon needle water loss at higher VPD. In other words, stomata respond to the prevailing balance between soil–plant water supply and the water demand by the atmosphere. As a result, there is an immediate closure of stomata as Ψ decreases (i.e., high stomatal sensitivity to drought, Section 3.5.2.1) in response to VPD. This phenomenon has been reported in Engelmann (Grossnickle and Reid 1985), black (Grossnickle and Blake 1986), and white (Grossnickle and Blake 1987*a*) spruce seedlings on reforestation sites, in controlled environment experiments with Norway spruce (Maier-Maercker 1998), and in mature white spruce trees (Goldstein et al. 1985) under natural forest conditions.

Net photosynthesis of spruce species also declines as VPD increases. For example, interior spruce seedlings have a decrease in P_n as VPD increases (Fig. 3.2*d*). Sitka (Sanford and Jarvis 1986) and white (Marsden et al. 1996) spruces are also reported to have a decrease in P_n with increasing VPD. Increasing VPD is thought to cause either g_{wv} to decline, as a guard against excessive plant water loss as P_n declines (Sharkey 1984), or P_n to decline, as a consequence of stomatal closure (Schulze et al. 1987). It is important to recognize

Fig. 3.2*c*. Relationship between needle conductance (g_{wv}) and shoot water potential (Ψ) for white spruce seedlings on a boreal reforestation site. Each point is an average of four seedling measurements (adapted from Grossnickle and Blake 1986).

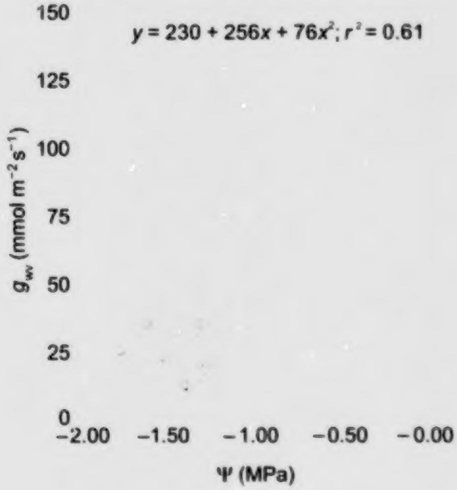
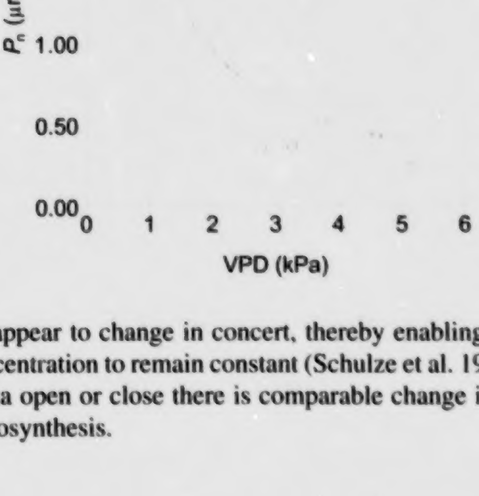


Fig. 3.2*d*. Net photosynthesis (P_n) of interior spruce seedlings in response to a range of summertime vapor pressure deficit (VPD) on a boreal reforestation site (adapted from Grossnickle and Major 1994*b*).



that P_n and g_{wv} appear to change in concert, thereby enabling the mesophyll-internal CO_2 concentration to remain constant (Schulze et al. 1987). This means that when stomata open or close there is comparable change in the mesophyll capacity for photosynthesis.

Growth of spruce species is related to the ability of cells to enlarge and cell division to occur under low levels of seedling water deficit (Section 2.1.3). As VPD increases, there is a decline in seedling Ψ (Fig. 3.2*a*), with a subsequent decrease in gas exchange (Figs. 3.2*b*, 3.2*d*). The direct effect of VPD on spruce seedling growth has recently been examined. Root growth of black spruce seedlings was reported to decline when seedlings were grown under high VPD (Darlington et al. 1997), while higher VPD was not reported to have any effect on the root growth of white spruce seedlings (Marsden et al. 1996). Interestingly, Marsden and associates (1996) found that bud flush of white spruce seedlings occurred earlier under low evaporative demand. Darlington and co-workers (1997) believe that the growth reduction attributed to high VPD was not related to increased production of the hormone ABA, but was probably the result of shoot water deficits. Northern latitude reforestation sites normally have high VPD over a portion of the growing season (Section 1.3.2). As a consequence, there are times during the growing season when VPD may be high enough to reduce spruce seedling growth.

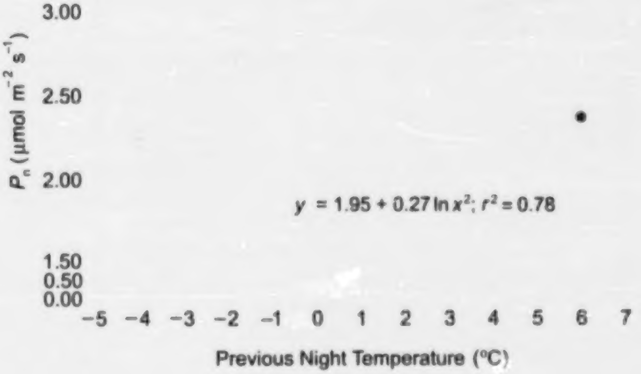
3.3 Air temperature

Spruce species have differing ranges of temperatures where maximum P_n occurs. Interior spruce seedlings reach 100% of maximum P_n at air temperatures between 15 and 23°C, inclusive (Fig. 3.3.2*a*). Sitka spruce is reported to have optimum P_n and g_{wv} between 18 and 22°C during the growing season (Ludlow and Jarvis 1971; Beadle et al. 1985*b*). During the summer, for both black (Lamhamedi and Bernier 1994; Rayment and Jarvis 1999) and Norway (Pisek et al. 1973) spruces, P_n is at an optimum between 10 and 20°C, while Engelmann spruce has a maximum P_n between 10 and 25°C (DeLucia and Smith 1987). This temperature range for maximum P_n rises and falls with seasonal temperature patterns. Open-field grown white spruce seedlings have a seasonal change in the temperature where maximum P_n occurs; this ranges from 15°C in the spring to 25°C in the summer and fall (Man and Lieffers 1997). Interestingly, when seedlings are grown under a vegetation cover, maximum P_n is similar to that for open-field grown seedlings during the spring and summer, although it declines to 15°C in the fall (Man and Lieffers 1997).

3.3.1 Low and freezing temperatures

Low and (or) freezing air temperatures occur throughout the year on northern latitude reforestation sites (Section 1.2.1) and can affect the performance of spruce seedlings in northern latitude forest plantations (Section 5.5.2). Low air temperature can reduce gas exchange of northern latitude spruce species during the growing season. The P_n of Engelmann spruce declines as the night air temperature decreases to −4°C (Fig. 3.3.1*a*). This slight decline in P_n at air temperatures that are just above and below freezing is also found in other spruce species (e.g., black: Lamhamedi and Bernier 1994; red: Schwarz et al. 1997; Sitka: Ludlow and Jarvis 1971, Neilson and Jarvis 1976). Maximum daily g_{wv} in

Fig. 3.3.1*a*. The maximum net photosynthesis (P_n) response of Engelmann spruce trees to the previous nighttime air temperature under warm soil temperature conditions (adapted from DeLucia and Smith 1987). Data on the photosynthetic response of trees that remained depressed for at least 3 days (i.e., June 30th) after exposure to the –4 °C were not included in the regression analysis (filled symbol).



Engelmann spruce also decreases when exposed to minimum air temperatures below 6°C (Smith 1985). Low early morning temperatures during the growing season (Section 1.2.1) can reduce the gas exchange capability of spruce species even when light and humidity levels are optimal.

Freezing temperatures during the summer can damage spruce species because they have low freezing tolerance during shoot elongation (Sections 3.7.4 and 5.4.3). Freezing during the growing season can also reduce the gas exchange processes of spruce species. Engelmann spruce have reduced g_{wv} after exposure to continual below-freezing minimum air temperatures (Kaufmann 1982*b*; Smith et al. 1984). The photosynthetic response of Engelmann spruce trees remains depressed for at least 3 days after exposure to –4 °C (Fig. 3.3.1*a*). After exposure to nighttime freezing conditions of –4 °C, black spruce has a dramatic reduction in P_n for both current and 1-year-old needles (Fig. 3.3.1*b*). A reduction in P_n also occurs in Engelmann spruce after exposure to below-freezing minimum air temperatures (DeLucia 1987; DeLucia and Smith 1987).

The freezing-induced reduction in P_n of spruce species during the growing season is believed to be due to damage of the photochemical process (Örlander 1993). Actively growing white spruce seedlings demonstrated photoinhibition and (or) photodamage after exposure to ~–5 to –6°C in newly flushed shoots, and after exposure to ~–11 to –12°C in dehardened 1-year-old shoots (Gillies and Binder 1997). Freezing damage becomes evident under high light because the photochemical process cannot effectively carry out the light reaction of photosynthesis. Damage from freezing temperatures can be exacerbated if spruce species are subsequently exposed to high light, as freezing can damage the

Fig. 3.3.1*b*. Response of current and 1-year-old needles of black spruce to a simulated summer frost (–4°C). The percent change in net photosynthesis (P_n) is expressed as a percentage of control trees (adapted from Dang et al. 1992).

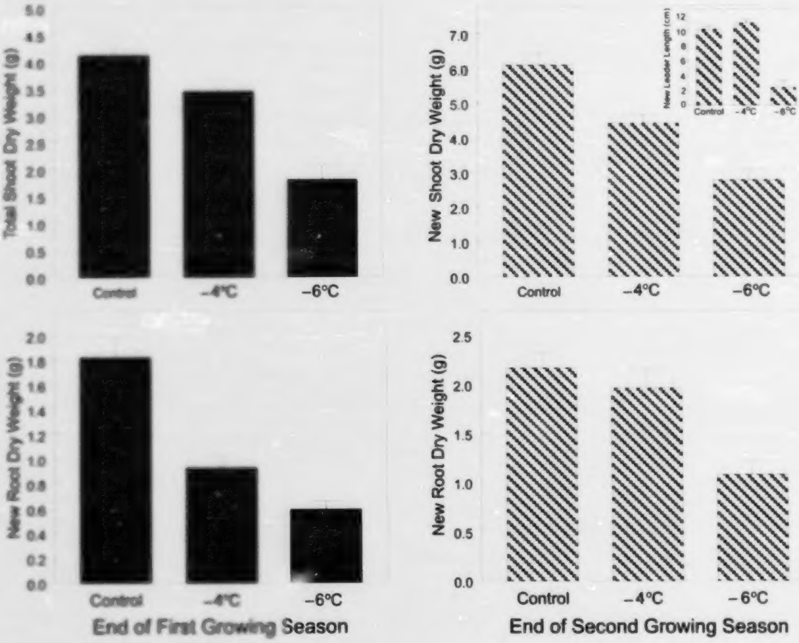
light-absorbing reaction centers. Normally, there is increased dissipation of absorbed light by protective quenching mechanisms (Ball 1994). These mechanisms usually minimize damage to the photochemical process when there is a limitation to the photosynthetic capacity of plants. When these light-absorbing action centers are damaged by freezing temperatures, the photochemical system is unable to process all incoming light energy, and photooxidative damage occurs. Consequently, spruce species can have a reduction in chlorophyll content in their needles (i.e., yellowing of needles) after exposure to freezing temperatures (Lundmark and Hällgren 1987). A number of studies have found that spruce species suffer greater damage to their shoots when they are exposed to the combined effects of freezing night temperatures followed by exposure to high light (Lundmark and Hällgren 1987; Örlander 1993). This combination of freezing night temperatures followed by exposure to high irradiance also causes a reduction in long-term shoot growth in Norway spruce (Welander et al. 1994). Freezing damage to foliage of conifer seedlings is more common on field sites where high light can cause the phenomenon of cold-induced photoinhibition (Ball 1994).

Summer frost can have a lasting effect on the performance of spruce species. In certain instances, substantial and irreversible reductions in P_n can occur after exposure to night air temperatures of –4 to –5°C during the growing season (Fig. 3.3.1*b*). In other instances, exposure to damaging frost can result in both g_{wv} (Dang et al. 1992) and photosynthetic capacity (Dang et al. 1992; Welander et al. 1994), taking up to ~10–20 days to recover to prefrost levels (Fig. 3.3.1*b*). The rate at which the gas exchange process recovers from frost can shift throughout the growing season; black spruce exposed to frost in May took 23 days for P_n to recover, while exposure to frost in August required 10 days for the recovery of P_n to prefrost levels (Lamontage et al. 1998). This shift in the gas exchange recovery process could be attributed, in part, to the progressive increase in freezing tolerance that occurs in spruce species during the latter part of the summer (Section 3.7).

This reduction in P_n in response to frost, during the summer growing season, does not always occur throughout other times of the year. Sitka spruce seedlings were found to be very sensitive to frost during late summer when P_n could be reduced to zero by a night frost, although in early winter, the photosynthetic capacity of hardened shoots continued after frost, as long as the root systems did not freeze and restrict access to soil water (Neilson et al. 1972). Tranquillini (1979) attributes this seasonal tolerance of P_n to frost to "hardening" characteristics that are related to the dormancy patterns of tree species growing in low-temperature climates.

Summer frosts can also damage newly planted seedlings and reduce plantation growth (Glerum and Paterson 1989; Stathers 1989; Krasowski et al. 1993*a*) (Section 5.4.3). This reduction in growth is due to the long-term effects of summer frost on the physiological performance of spruce seedlings, which affects their growth capability. In one example, interior spruce seedlings were exposed to a frost in midsummer, after budset had occurred (Fig. 3.3.1*c*). Exposure to frost caused a reduction in both shoot and root development at the end of the first growing season, with a more severe frost causing a greater reduction in growth.

Fig. 3.3.1*c*. Morphological development (i.e., shoot and root dry weights, and new leader growth) of 2+0 interior spruce seedlings ($N = 20$: mean + SE) over two growing seasons that were either not exposed to frost (i.e., control) or after exposure to either a −4 or −6°C frost during midsummer. Seedlings were exposed to the frost 4 weeks after budset, during the first field growing season (Folk and Grossnickle, unreported data).



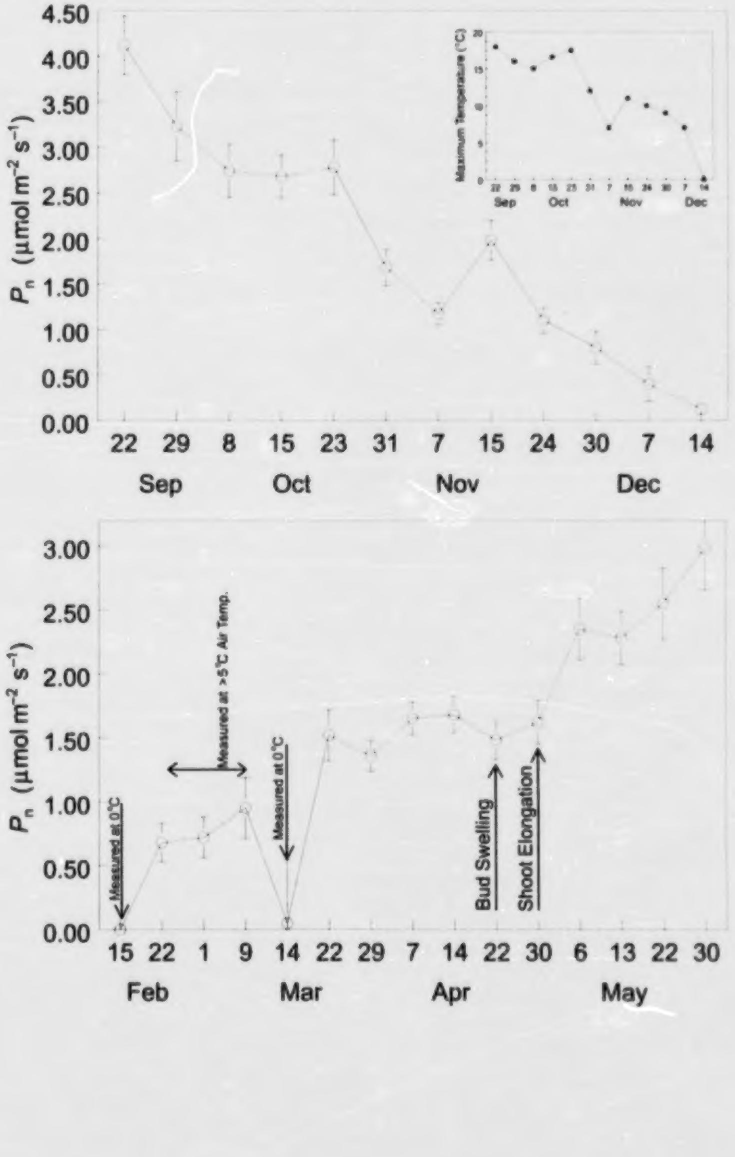
In addition, exposure to a single midsummer frost altered seedling development in the subsequent growing season. Exposure to a –4 °C frost had no effect on new leader growth, although new shoot and root biomass were reduced over the next growing season. In contrast, exposure to a –6°C frost caused a large reduction in shoot and root development over the next growing season. Implications of these findings are twofold. First, exposure of spruce species to frost when they have a low level of freezing tolerance can reduce the long-term growth capability of seedlings. Second, during the summer growing season, spruce species have a low level of freezing tolerance (Section 3.7.4), and only a slightly more severe frost (i.e., –6 versus –4 °C) can cause a dramatic reduction in subsequent growth capability over at least two growing seasons. This example shows how the exposure of newly planted spruce seedlings to just a single frost can have a major impact on their ability to grow.

Seasonal patterns of P_n in spruce species are tied, in part, to the seasonal temperature patterns. During fall, the photosynthetic capacity of spruce species declines (Vidaver et al. 1989; Binnie et al. 1994; Binder and Fielder 1996*a*; Schaberg et al. 1998; Man and Lieffers 1997*a*) (Fig. 3.3.1*d*). This decline of P_n in the fall for spruce is due to low air and soil temperatures (Tranquillini 1979; Schwarz et al. 1997*a*). A decline in g_{wv} also occurs in Engelmann spruce during the fall and is directly related to minimum air temperatures of the preceding night (Smith et al. 1984). The fall decline in P_n is also partly due to the dormant state of spruce species, resulting in a lower demand for photosynthates that are required for growth (Section 2.2.3). In addition, the fall and winter decline in P_n is also attributed to the disorganization of the chloroplasts and the breakdown in chlorophyll (Kozlowski et al. 1991), which is known to occur in spruce species (Section 2.6.1.4). These structural and biochemical changes to the chloroplasts are part of a seasonal resistance to permanent freezing temperature damage (Havranek and Tranquillini 1995).

Under the conditions of low and freezing winter temperatures, the P_n of spruce species remains very low (Bourdeau 1959; Schaberg et al. 1995, 1996). This winter depression of photosynthesis during freezing is due to a reduction in the capability of the photochemical system to process incoming light energy (Bolhàr-Nordenkampf and Lechner 1988; Strand 1995). During winter thaws, P_n increases within a few days (Schaberg et al. 1998). In some instances, P_n in spruce species can reach levels that are comparable to those measured during the growing season (Tranquillini 1979; Schaberg et al. 1995, 1996; Strimbeck et al. 1995), while in other instances, P_n increases to only ~33% of growing season values (Fig. 3.3.1*d*) (Schaberg et al. 1998). This indicates that spruce species are able to take advantage of a winter thaw and replenish needle carbon stores, thus partially offsetting the metabolic cost (i.e., maintenance respiration) of retaining needles throughout the winter.

An increase in P_n does occur in spruce species during the spring (e.g., Fig. 3.3.1*d*) and is attributed to a number of factors. An increase in soil

Fig. 3.3.1*d*. Fall, late winter, and spring net photosynthesis (P_n) patterns of interior spruce seedlings ($N = 10$: mean ± SE) in an outdoor compound located in southern coastal British Columbia. All P_n readings were taken at a photosynthetically active radiation level of 1000 µmol m^{-2} s^{-1}. Maximum daytime temperatures are given for each measurement day in fall and winter. Most springtime gas exchange measurements were taken on days when air temperatures exceeded 10°C. Bud swelling occurred on April 22, with shoot elongation continuing through the remainder of the spring measurements (Grossnickle and Fan, unreported data).



temperatures is known to cause an increase in P_n, although increases in air temperature are also important (Jurik et al. 1988; Lundmark et al. 1988; Day et al. 1989; Man and Lieffers 1997*a*; Schwarz et al. 1997; Wang and Zwiazek 1999*a*). The recovery of gas exchange processes in the spring appears to be dependent upon the resumption of an adequate supply of soil water as soils thaw (Havranek and Tranquillini 1995). The late-winter and early-spring increase in P_n can also be attributed to the de novo synthesis of photosynthetic pigments, from winter lows to springtime maximum levels (Section 2.6.1.4). Continued increases in P_n during the spring also occur as the shoots become active, indicating an increased demand for photosynthates required for growth.

3.3.2 High temperature

Northern latitude reforestation sites can have high soil surface temperatures and air temperatures near the ground during the growing season. These high temperatures are related to the removal of the forest canopy, which allows solar radiation to reach the soil surface, thereby shifting the solar energy to both the air near the soil surface and the soil surface (Sections 1.2 and 1.4). When seedling damage or mortality in the field is attributed to high temperature, soil surface temperature is the single most important factor. The effect of high soil temperature on seedling performance on reforestation sites is discussed in detail in Section 5.4.4.

Gas exchange capability of spruce species can be influenced by increased air temperatures. At air temperatures above 23°C, P_n of interior spruce seedlings drops sharply, tapering off at 30°C and ceasing altogether at 35°C (Fig. 3.3.2*a*). In general, spruce species have a decrease in P_n above ~20°C, and very low or no P_n at temperatures >35–40°C (Ludlow and Jarvis 1971; Meng and Arp 1993; Lamhamedi and Bernier 1994; Vann et al. 1994; Alexander et al. 1995). The photosynthetic capacity of spruce is adversely affected by air temperatures higher than ~25°C.

High temperatures can occur in the absence of other environmental stresses, although it is more common in combination with low relative humidity and high light level, plus seedling water stress. The effects of heat stress are therefore often confounded with those of water stress. The combination of these factors has a much greater potential to inhibit the photosynthetic process than does high temperature alone.

Heat damage can occur through direct exposure to high air temperatures or through the accumulation of heat stress over a period of time (Levitt 1980). Northern latitude conifer species are susceptible to high and extreme temperature damage. Unhardened black spruce seedlings are damaged at a temperature of 36°C after 3 h of exposure (Koppenaal et al. 1990). Constriction of a collar of bark at ground level ("heat girdling") occurs in field-planted spruce seedlings at soil surface temperatures above 46°C (Tranquilini 1979). At extreme temperatures, spruce seedling damage can occur after less exposure time (Fig. 3.3.2*b*). Black spruce seedlings exposed to 44°C required almost 2 h before damage

Fig. 3.3.2*a*. Percent change in net photosynthesis (P_n) of white spruce seedlings ($N = 10$) in response to high air temperatures at a constant VPD (Grossnickle and Folk, unreported data).

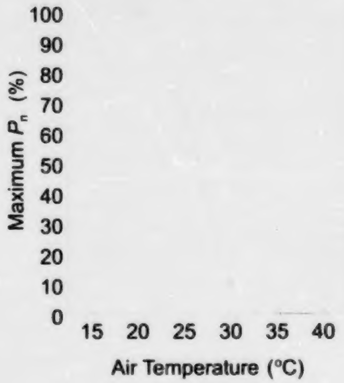
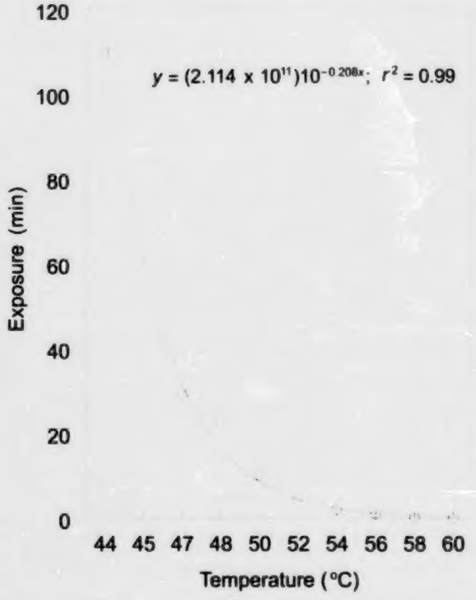


Fig. 3.3.2*b*. Temperature and duration of heat exposure, resulting in indirect damage (detected 3 weeks after heat treatment) to 50% of the needles of first-year black spruce seedlings (adapted from Colombo and Timmer 1992).



occurred, while seedlings were damaged after less than 10 min at temperatures above 50°C (Colombo and Timmer 1992). On the other hand, if boreal conifer seedlings are exposed to a heat shock (i.e., supraoptimal temperatures), they develop increased thermotolerance (Koppenaal et al. 1990).

There is also a seasonality and needle age phenomenon related to the level of heat tolerance in conifer seedlings. Heat tolerance, low in new needles of conifer seedlings, increases as new needles mature (Burr et al. 1993). In addition, current-year needles have less heat tolerance than older needles (Koppenaal and Colombo 1988; Burr et al. 1993).

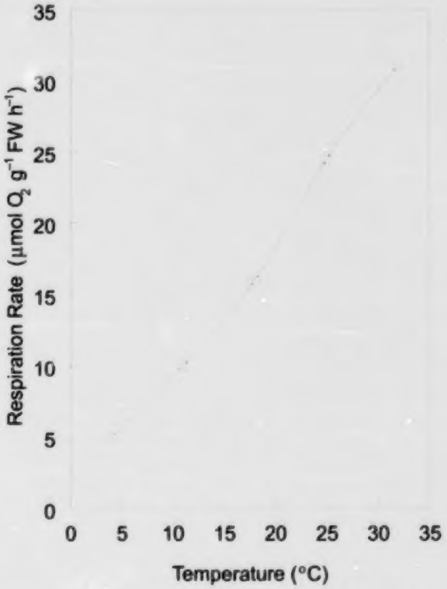
3.3.3 Temperature and respiration

Temperature is the primary environmental variable influencing maintenance respiration (Section 2.2.4). Both preplant handling and storage practices, and various reforestation site silvicultural practices, can affect spruce seedling exposure to a range of temperatures. Any of these practices that affect temperatures influence spruce seedling respiration rates.

Warm temperatures increase the use of photosynthates for maintenance respiration in conifer species. This decreases the availability of these reserves for seedling growth. For example, Engelmann spruce has a Q_{10} (Section 2.2.4) of 2 (Sowell and Spomer 1986) to 2.8 (Ryan 1990), while black spruce Q_{10} ranges from 1.5 to 1.8 (Lavigne and Ryan 1997) during the growing season. Actively growing white (Fig. 3.3.3), black (Lamhamedi and Bernier 1994), red (Alexander et al. 1995), and Norway (Stockfors and Linder 1998) spruces have a continual increase in respiration rates at temperatures of up to 30–40°C. At the same time that respiration rates for spruce species are increasing rapidly, there is a decline in P_n (e.g., Fig. 3.3.2*a*). For example, Norway spruce has respiration rates well above their photosynthetic capacity at 30°C (Larcher 1969). As temperature increases, the ability of spruce seedlings to produce photosynthates declines, and valuable photosynthates are used for maintenance respiration rather than growth. If high air temperatures were to persist, seedling growth would be reduced.

Shoot respiration rates are reported to change throughout the growing season for spruce species. For white spruce seedlings, the rates were higher in the spring, at any given temperature, compared to the summer and fall (Man and Lieffers 1997). Black spruce stem (Lavigne and Ryan 1997) and shoot (Rayment and Jarvis 1999) respiration rates reached a peak during the growing season. Norway spruce trees have a variation in Q_{10} across the growing season, with a high of 2.55 in June and a low of 1.92 in August (Stockfors and Linder 1998). Man and Lieffers (1997) attributed these higher springtime shoot respiration rates to two factors. First, white spruce seedlings require maintenance respiration to repair biological systems (e.g., photosynthetic systems) damaged during the winter. Second, white spruce seedlings require construction respiration to allow springtime shoot development to occur. The timing of these higher respiration rates correspond to the springtime increase in P_n (Fig. 3.3.1*d*). The

Fig. 3.3.3. Rate of total dark respiration of white spruce roots at a range of measurement temperatures (adapted from Weger and Guy 1991). Root fresh weight is abbreviated as FW.



springtime increase in P_n indicates an increased demand for photosynthates required for maintenance and construction respiration in spruce species.

During the fall as air temperatures decline, respiration rates also decline (Bourdeau 1959; Tranquillini 1979). This can be seen in the respiratory decline of black spruce when average nighttime temperatures decrease from 15 to –6°C, with no respiration occurring at nighttime temperatures below –6°C (Rayment and Jarvis 1999). Throughout the winter, when air temperatures are low, respiration rates are minimal for spruce species (Bourdeau 1959; Tranquillini 1979; Benecke 1985). Black spruce stem respiration decline when trees are dormant (Lavigne and Ryan 1997). Havranek and Tranquillini (1995) consider the low respiration rates of conifers during winter dormancy to be an adaptive strategy to minimize carbon loss during long boreal winters. Even though respiration rates are low during the winter, the continuous low winter respiration has been estimated to be ~7% of the annual carbon gained through photosynthesis in conifers (Tranquillini 1979). As spruce seedlings emerge from snow in the spring, P_n during the springtime is required to generate most photosynthates needed for growth because of this loss of stored assimilate.

3.3.4 Temperature and shoot growth

Shoot growth is dependent upon efficient metabolism and the synthesis of new tissue. The range of optimal temperature for both photosynthesis and dry matter production, as a rule, is no wider than 10°C and is related to the natural thermal climate of the species (Larcher 1995). This optimal growth temperature is the point where maximum growth processes proceed, yet development remains in balance. The optimum temperature can be different, depending upon the growth parameters being defined.

White spruce seedlings have optimal shoot growth when day–night temperatures are kept at 18–22°C (Brix 1972; Heninger and White 1974; Tinus and McDonald 1979), while Engelmann spruce (from a Colorado seed source) has optimal shoot growth when day–night temperatures are 19–23°C (Hellmers et al. 1970). Norway spruce has optimum shoot growth between a general range of 18–24°C (Heide 1974*b*). Shoot growth reaches an optimal level for Sitka spruce when air temperatures are maintained between 20 and 25°C (Coutts and Philipson 1987). Interestingly, optimum black spruce seedling height growth occurs at a higher day–night temperature range (24–28°C) than other spruce species, although maximum shoot mass occurs at day–night temperatures (22–24°C) comparable to other spruce species (Odlum and Ng 1995). Needle initiation and bud development in spruce species have an optimum temperature of at least 20–25°C, and initiation is much slower below 20°C (Section 2.6.1.1). These findings indicate that, in general, shoot growth patterns for spruce species are at their optimal levels when air temperatures are between 18 and 25°C.

3.4 Wind

Wind speeds are greater on open reforestation sites in comparison to closed forest canopies (Section 1.4). Wind can have an effect on the g_{wv} response of seedlings. This effect on g_{wv} occurs because increasing wind speeds reduce the boundary layer conductance (Section 2.1.2) and needle temperature (Section 2.6.1.3) of spruce needles. However, very few direct studies are reported on the effects of wind on conifer stomatal response. Increased wind speed causes a decrease in g_{wv} of Sitka spruce (Grace et al. 1975) and transpiration rates of Norway spruce seedlings (Tranquillini 1979; Baig and Tranquillini 1980). This reduction of stomatal opening, in response to increased wind speed, can cause up to a 10% reduction in the P_{n} of Norway spruce (Tranquillini 1979).

The decrease in g_{wv} or transpiration with increasing wind speed can be caused by a number of factors. Since spruce needles are small, wind speed can decrease the boundary layer resistance, thereby increasing the advective dissipation of heat from the needles and increasing the transfer of water vapor between the substomatal cavity and the air (Gates 1976). Since the air always has a greater VPD than the substomatal cavity, increased wind can increase VPD around the needle stomata, causing a reduction in g_{wv}. Stomata of Norway spruce needles close when the needle surface is dehydrated, as a result of wind, even when the needles have a high water content (Tranquillini 1979). Other possible causes for the reduction in g_{wv} or transpiration with an increase in wind speed include a higher CO_2 concentration around the stomata, alteration of stomatal water relations, and possible vibrational effects on stomatal response (Burrows and Milthorp 1976).

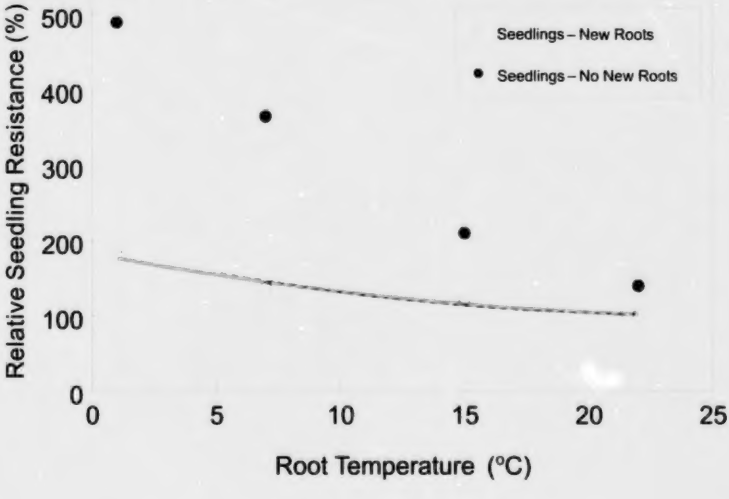
3.5 Soil

3.5.1 Soil temperature

Low soil temperatures throughout the growing season are considered one of the major constraints in establishing seedlings on boreal reforestation sites (Stathers and Spittlehouse 1990). Low soil temperature is also a primary factor limiting physiological performance during the early part of the growing season of conifer species in subalpine forests in the mountains of western North America (Smith 1985). Low soil temperature places stress on newly planted spruce seedlings by affecting their water movement capability, gas exchange, and subsequent root growth. This in turn affects seedling growth and survival on northern latitude reforestation sites (Section 5.5.2).

Seedlings can have restricted water uptake in cold soils even if there is adequate water available within the soil profile. White spruce seedlings with an actively growing root system have an increase in relative seedling resistance to water flow as root temperature decreases (Fig. 3.5.1*a*). This increase in seedling resistance to water flow parallels the increase in the viscosity of water as root temperature increases. Seedlings with no new roots have dramatically greater relative seedling resistance to water flow at colder soil temperatures. The large

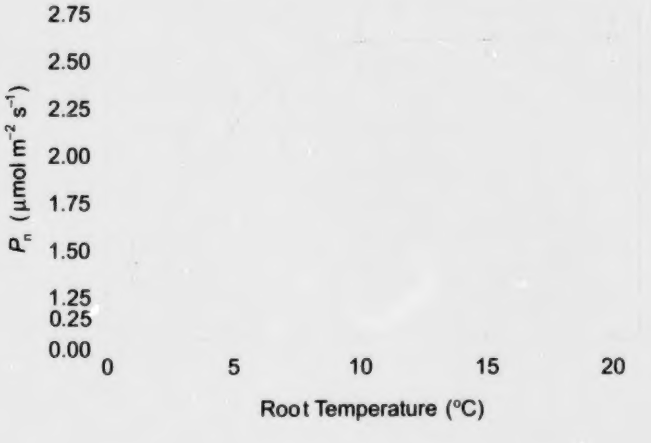
Fig. 3.5.1*a*. The effect of temperature on relative viscosity of water (gray line) and the effect of root temperature on the relative resistance to water flow through the SPAC pathway for white spruce seedlings (i.e., relative to seedlings with white roots measured at 22°C). Seedlings measured had either no new root development or actively growing roots (adapted from Grossnickle 1988*a*).



difference in water flow at low temperatures between seedlings with no new roots and seedlings with extensive new root development occurs because new unsuberized roots are more permeable compared to older suberized roots (Section 2.1.2) and because of an increase in new root absorbing surface area. An increase in plant resistance to water flow with colder soil temperatures has been found to occur in Engelmann (Kaufmann 1975) and white (Day et al. 1990) spruce trees and seedlings (Grossnickle and Blake 1985; Grossnickle 1988*a*). As soil temperatures warm up, spruce species have an improved water uptake capability, which is attributed to the decreased viscosity of water, greater root permeability, and increased root growth (Kaufmann 1975; Häussling et al. 1988).

Gas exchange processes of spruce seedlings are not affected by the moderate soil temperatures that are typically found on northern latitude reforestation sites during the growing season (Section 1.2.1). At root temperatures above 10°C, there is very little effect of root temperature on the P_n of Engelmann spruce seedlings (Fig. 3.5.1*b*). However, at root temperatures below 10°C, Engelmann spruce seedlings show a decrease in P_n. A decrease in both g_{wv} (Nielson and Jarvis 1976; Smith 1985; DeLucia 1986; Grossnickle 1988*b*; Carter et al. 1988; Landhäusser et al. 1996) and P_n (Tranquillini 1979; Nielson and Jarvis 1976; DeLucia 1986; DeLucia and Smith 1987; Vapaavuori et al. 1992; Landhäusser et al. 1996) occurs as root temperatures drop below approximately 8°C for spruce species. The seasonal decline of P_n in the fall and increase in the spring (Section 3.3.1) has been attributed, in part, to changes in soil temperatures (Schwarz et al. 1997). The effect of root temperature on gas exchange processes is not simply a response to severe water stress but indicates the operation of a mechanism that curtails water loss through stomatal closure before severe water stress develops (Teskey et al. 1984).

Fig. 3.5.1*b*. Effect of root temperature, at a constant shoot temperature, on net photosynthesis (P_n) of Engelmann spruce seedlings (adapted from DeLucia 1986).



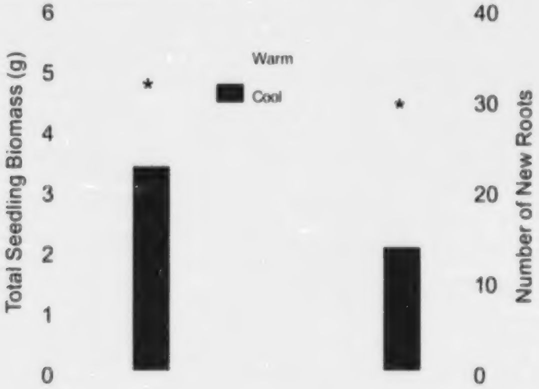
Snow cover can persist on northern latitude reforestation sites for up to 8 months throughout the year (Section 1.2.1). The effect of late snow cover in the spring can alter the gas exchange patterns of spruce. A late-spring snow cover can maintain cold soil temperatures (<1°C) which prolong low P_n in spruce trees (Day et al. 1989). This late-spring snow cover can cause a reduction in the capability of spruce seedlings to initiate photosynthesis early in the growing season.

Root growth is reduced by low soil temperatures. Root elongation for both white and black spruce seedlings increased from 0.5 mm day^{-1} to a high of 1.5–2.0 mm day^{-1} as soil temperature (at 10 cm) increased from 2 to 12°C (Tryon and Chapin 1983). Soil temperatures of 3°C consistently caused a reduction in root growth (Husted and Lavender 1989). Norway spruce seedlings have reduced root growth at soil temperatures between 5 and 8°C (Vapaavuori et al. 1992). These findings are consistent with other studies showing that low root temperatures reduce root growth of coniferous species (Stone and Schubert 1959; Lyr and Hoffman 1967; Nambiar et al. 1979; Grossnickle and Reid 1983; Tyron and Chapin 1983; Grossnickle and Blake 1985; Sutton 1991).

Root growth increases as soil temperatures rise above 10°C. Root biomass increased by 30% in black spruce seedlings between soil temperatures of 3 and 15°C, while shoot mass was unaffected; this caused an increase in the root to shoot ratios of the seedlings (Landhäusser et al. 1996). Soil temperatures between 10 and 17°C, compared to low soil temperatures, allowed for improved, although variable, root growth of white spruce seedlings (Husted and Lavender 1989). Root growth for white and black spruce seedlings was higher at a soil temperature of 22°C than at 10°C (Grossnickle and Blake 1985). Norway spruces also have good root growth between 12 and 20°C (Lyr and Hoffman 1967). Black spruce seedlings have maximum root growth at day–night temperatures of 21–19°C (Odlum and Ng 1995). White spruce is reported to have optimum root growth at a soil temperature of 19°C (Heninger and White 1974). Root growth was greatest in Sitka spruce under a 25–20°C day–night temperature regime (Binder et al. 1990). These findings indicate that, in general, root growth for spruce species are at reasonable levels when root temperatures are above ~12°C, with optimum root growth occurring around 20°C.

Low soil temperatures, in the effective root zone, during the growing season cause reduced growth in newly planted spruce seedlings in northern latitude locations. For example, soil temperatures of 7.5–12°C are typical of the boreal forests during portions of the growing season (Section 1.2.1). In addition, soils that have thick surface organic horizons have colder underlying mineral soil horizons because of poor heat transfer (Section 1.2.4). Spruce seedlings planted into soils having these thick organic surface layers have substantially reduced shoot and root growth (Fig. 3.5.1*c*). This can have a tremendous influence on early establishment of recently planted seedlings. Intense vegetation competition causes seasonally low soil temperatures and is one of the primary environmental factors limiting spruce seedling growth on northern latitude sites (Section 5.5.2).

Fig. 3.5.1c. Growth of Engelmann spruce seedlings over one growing season (June 9 – September 16) on a high-elevation reforestation site (1450 m in central British Columbia, 52° N lat.) in response to cool (12.7°C) and warm (20.5°C) seasonal soil temperatures (–10 cm) (adapted from Balisky and Burton 1997). The * indicates a significant difference at the 5% level, based on an ANOVA and a Student–Newman–Keuls multiple comparison test.



3.5.2 Soil water

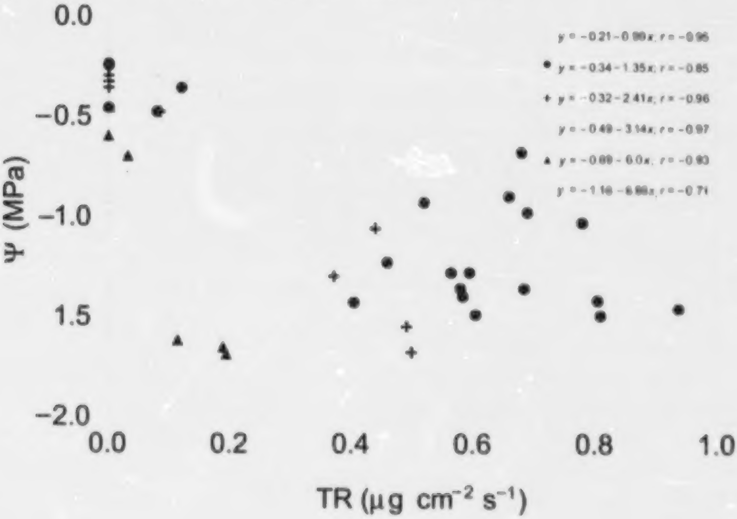
The availability of soil water is one of the most critical environmental parameters that is required for the successful establishment of spruce seedlings. As previously stated, water is essential for the normal functioning of plants (Section 2.1). Either too little or too much water can limit the physiological processes of spruce species and their subsequent morphological development. This section examines how drought or flooded soil influences the performance of spruce species.

3.5.2.1 Low soil water

Drought causes water deficits in seedlings by restricting water uptake from the soil. Under drought, soil hydraulic conductivity is reduced, and the rate of water movement through the soil profile to the seedling root system is restricted (Section 1.3.1). Figure 3.5.2.1*a* shows how Engelmann spruce seedlings have increased resistance to water flow through the SPAC due to greater drought (i.e., lower Ψ_{pd}), limiting the ability of root systems to access water from the soil system. As a result, relative resistance increases because the seedling root system is unable to take up sufficient water from the surrounding soil to meet the evaporative demands placed upon the shoot system by the atmosphere (Elfving et al. 1972; Hinckley and Bruckerhoff 1975; Sterne et al. 1977).

Another source of increased resistance to water movement through the SPAC during severe drought stress is the cavitation of xylem conducting tissues (Section 2.1.2). When water stress becomes severe enough (–2.0 to –3.0 MPa), spruce species xylem elements begin to embolize, resulting in a loss of a portion of the hydraulic conductivity of the xylem water conducting system (Borghetti et

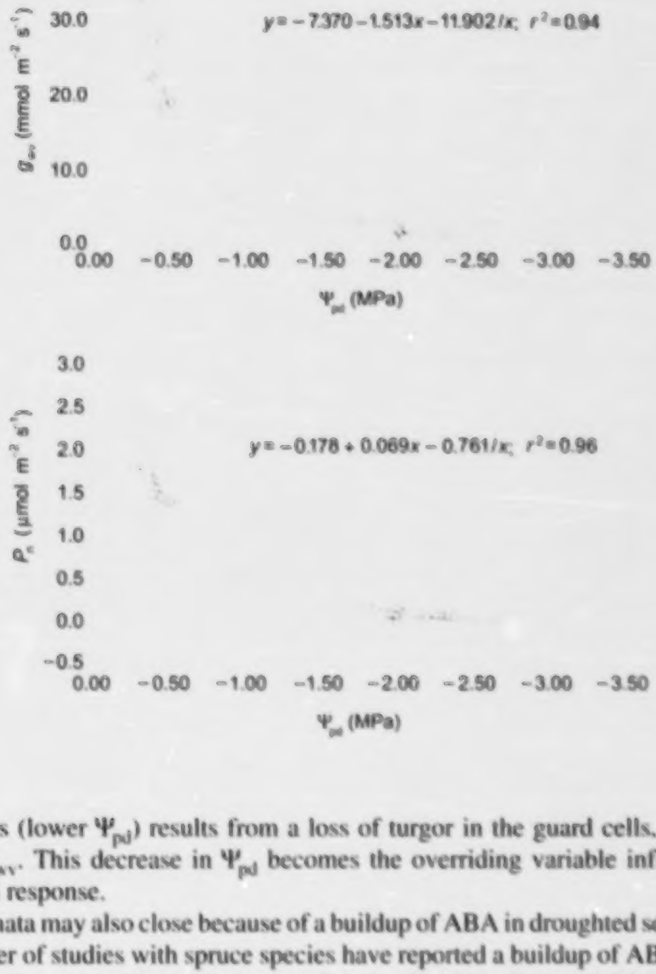
Fig. 3.5.2.1*a*. Relationship between transpiration rate (TR) and shoot water potential (Ψ) for Engelmann spruce seedlings under a range of drought (adapted from Kaufmann 1979). Regression lines were not plotted for seedlings under the greatest water stress; rather, data points were connected by arrows for the sequence by which they were determined from morning to evening.



al. 1989; Sperry and Tyree 1990). This phenomenon can result in a permanent increase in the resistance to water movement through the existing xylem conducting system, which can only be relieved by the production of new xylem elements. Temporary relief can occur under conditions of optimum soil water or low evaporative demand. Thus, water stress levels that can occur just after planting spruce seedlings in the field (Grossnickle and Reid 1984*b*; Grossnickle and Heikurinen 1989; Draper et al. 1985) (Section 5.3) can cause cavitation of xylem elements and have long-lasting effects on seedling water balance on reforestation sites (Kavanagh and Zaerr 1997).

Limited soil water can cause plant water stress and reduce the gas exchange processes in spruce seedlings. Thus, it is not surprising that the degree of stomatal opening that occurs in interior spruce seedlings is related to predawn Ψ (Fig. 3.5.2.1*b*). At high predawn shoot water potential (Ψ_{pd}), there is much variation in g_{wv}, and this can be related to variations in air temperature (Section 3.3), light (Section 3.1), and evaporative demand (Section 3.2). For spruce, g_{wv} decreases as Ψ_{pd} declines, with nearly complete stomatal closure at <–2.0 MPa. Rapid stomatal closure with declining Ψ_{pd} can occur in white (Grossnickle and Blake 1987*a*; Grossnickle and Heikurinen 1989) and Engelmann (Lopushinsky and Klock 1974; Kaufmann 1979; Grossnickle and Reid 1985) spruce seedlings planted in the field. Interestingly, the stomata of Engelmann spruce are more sensitive to needle water stress than other conifer species found in their associated ecological range (Lopushinsky 1969). Stomatal closure in droughted

Fig. 3.5.2.1*b*. Response of needle conductance (g_{wv}) and net photosynthesis (P_n) to changes in predawn shoot water potential (Ψ_{pd}) for interior spruce seedlings (adapted from Grossnickle and Fan 1999).



seedlings (lower Ψ_{pd}) results from a loss of turgor in the guard cells, causing lower g_{wv}. This decrease in Ψ_{pd} becomes the overriding variable influencing stomatal response.

Stomata may also close because of a buildup of ABA in droughted seedlings. A number of studies with spruce species have reported a buildup of ABA in the shoots during drought (Roberts and Dumbroff 1986; Tan and Blake 1993; Jackson et al. 1995). Abscisic acid is a natural plant hormone that interacts with physiological processes related to stress avoidance in conifers, such as the promotion of stomatal closure (Davies 1995). This response is a classic dehydration avoidance strategy whereby stomatal closure during soil drought allows plants to conserve shoot water (Pallardy et al. 1995) (Section 2.1.3).

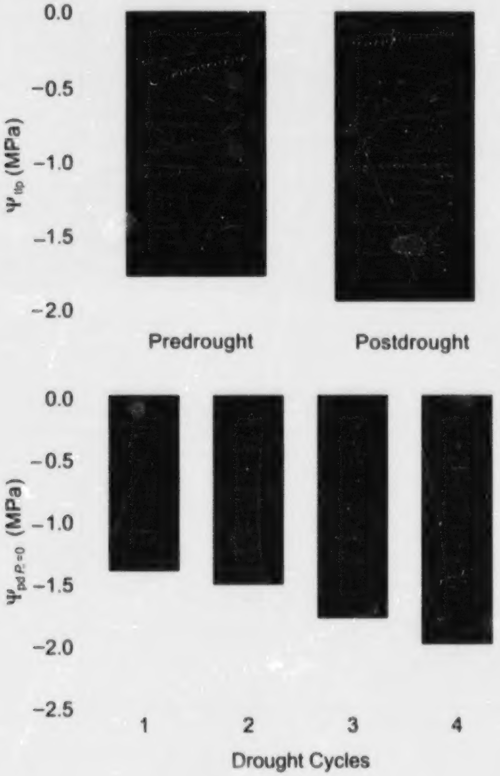
Limited soil water also causes a decrease in P_n. Net photosynthesis decreases as Ψ_{pd} declines, with P_n decreasing to the compensation point between −2.0 and

–2.5 MPa (Fig. 3.5.2.1*b*). A decrease in P_n with declining Ψ_{pd}, with P_n decreasing to the compensation point between a Ψ_{pd} of –2.0 to –3.0 MPa, is reported for many spruce species (e.g., black: Patterson et al. 1997; interior: Grossnickle and Major 1994*a*, Eastman and Camm 1995, Fan et al. 1997; red: Seiler and Cazell 1990; Sitka: Watts and Neilson 1978, Fan et al. 1997; white: Brix 1979, Patterson et al. 1997). When compared to associated species (i.e., *Pinus*, *Populus*, *Betula*), spruce showed the greatest reduction in photosynthesis under moderate drought (Jarvis and Jarvis 1963*a*). In narrow-leafed conifers, stomatal closure during low to moderate drought is considered the primary factor limiting photosynthesis (Brodribb 1996). Both g_{wv} and P_n decreased in parallel as Ψ_{pd} declined, indicating that stomatal limitation is a primary factor causing the reduction of P_n for spruce species during the initial stages of drought. Under severe drought, nonstomatal limitations to P_n (i.e., mesophyll limitations) become increasingly more important than stomatal limitations in spruce (Beadle et al. 1981; Stewart et al. 1995), as further drought stress limits the transfer of CO_2 into the chloroplasts and limits the actual fixation of CO_2. As water stress becomes even more severe, the primary photochemistry is down-regulated in interior spruce seedlings (Eastman and Camm 1995) as a mechanism to protect chloroplasts from photodamage.

Spruce species have a number of mechanisms to tolerate drought stress. As stated previously, drought tolerance of a species is primarily determined by the maintenance of turgor, possibly through solute accumulation, or through desiccation tolerance via chloroplast resistance to drought (Section 2.1.3). The examples presented below show the combination of physiological responses used by spruce species to tolerate drought.

Spruce species are able, in certain instances, to undergo osmotic adjustment in response to drought. For example, interior spruce seedlings undergo a moderate level of osmotic adjustment after exposure to drought (Fig. 3.5.2.1*c*). A number of studies have reported that spruce species exposed to drought undergo either no or only a slight level of osmotic adjustment (Seiler and Cazell 1990; Roberts and Cannon 1992; Zine El Abidine et al. 1994*a*; Jackson et al. 1995), while other studies have reported a large level of osmotic adjustment (Buxton et al. 1985; Zwiazek and Blake 1989, 1990*a*; Zwiazek 1991; Tan et al. 1992*b*). Osmotic adjustment is a major form of drought tolerance in tree species (Abrams 1988), and this osmotic adjustment is due to the accumulation of solutes. Spruce species vary in their ability to use osmotic adjustment as a way to increase drought tolerance. Spruce species can have a large change in Ψ_π, which is dependent upon their phenological stage of development (Section 2.1.1). Interestingly, all the above reported cases showing a large change in Ψ_π occurred in droughted spruce seedlings, in comparison to nondroughted seedlings, that had been actively growing just prior to drought, while the cases showing no or only a slight change in Ψ_π occurred in seedlings that did not have active shoot growth. It seems that the ability to undergo large amounts of osmotic adjustment in spruce species is tied to the phenological stage the seedlings are in when exposed to a drought.

Fig. 3.5.2.1*c*. Changes in drought tolerance (mean – SE) of interior spruce seedlings in response to drought. Drought tolerance was determined by both (*i*) the osmotic potential at turgor loss point (Ψ_{tlp}) before and after a single drought and (*ii*) the level of drought stress (defined by predawn shoot water potential (Ψ_{pd})) required for net photosynthesis (P_n) to decrease to 0 over a series of drought cycles (adapted from Fan and Grossnickle 1998).

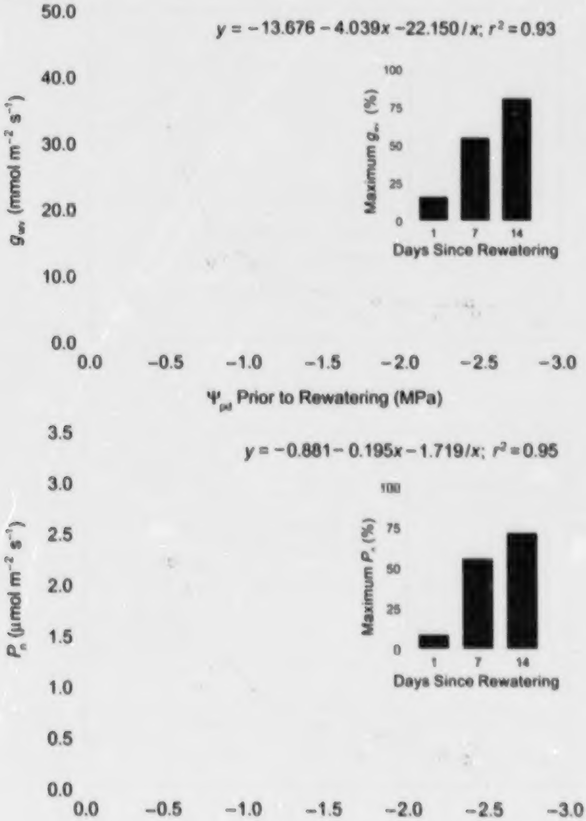


Spruce seedlings exposed to repeated drought also have higher cell wall elasticity which allows turgor pressure to be maintained as water stress increases (Blake et al. 1991; Zwiazek 1991; Marshall and Dumbroff 1999). This higher cell wall elasticity increases the potential for turgor maintenance as RWC declines. This drought resistance strategy can help spruce species because they inherently have low cell wall elasticity (Section 2.1.1).

Spruce species also develop photosynthetic capability that is resistant to drought. For example, interior spruce seedlings were able to continue photosynthesizing at greater drought stress after exposure to a series of drought stress events; P_n decreased to 0 at a Ψ_{pd} of −1.41 MPa after the first drought, but P_n decreased to 0 at a Ψ_{pd} of −2.0 MPa after a series of four droughts (Fig. 3.5.2.1*c*). Black spruce seedlings preconditioned with water stress also have a higher P_n than unconditioned seedlings under drought conditions (Zine El Abidine et al. 1994*a*). This ability to maintain P_n after exposure to drought occurs even though the chlorophyll content of spruce needles may decline after drought (Buxton et al. 1985). Tree species adapt to drought by developing a level of tolerance that enables the continuation of photosynthesis under drought (Abrams 1994).

Even though spruce species have the ability to both avoid and tolerate stress that is related to drought, this stress can alter subsequent seedling performance. The rate of physiological recovery is dependent upon the severity of the drought. In this example, as the severity of drought increased, the rate of gas exchange recovery decreased after the seedlings were rewatered (Fig. 3.5.2.1*d*). In both interior spruce (Fig. 3.5.2.1*d*) and black spruce (Zwiazek and Blake 1989), prior

Fig. 3.5.2.1*d*. Needle conductance (g_{wv}) and net photosynthesis (P_n), measured 1 day after rewatering (i.e., Ψ_{pd} of >−0.5 MPa), for interior spruce seedlings in response to predawn shoot water potential (Ψ_{pd}) taken at the end of a drought. The insert figures represent the percent recovery of g_{wv} and P_n, when compared to optimum soil water, over 14 days after exposure to a severe (i.e., Ψ_{pd} of <−2.0 MPa) drought (adapted from Grossnickle and Fan 1999).

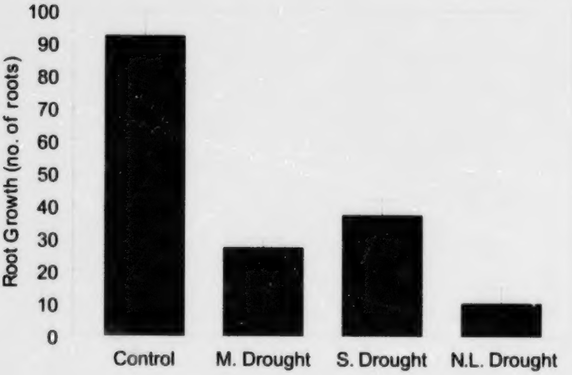


exposure to water stress resulted in lower g_{wv} and thus enhanced stomatal sensitivity as shoot Ψ declined. After a severe drought (i.e., predawn Ψ of <–2.0 MPa), g_{wv} slowly recovered after rewatering, although g_{wv} only reached 80% of predrought stress g_{wv} after 14 days. This indicates that interior spruce has a well-developed response for avoidance of water stress through enhanced stomatal sensitivity, although it has a poor capability to respond rapidly after relief from severe drought. For P_n, low levels of water stress (i.e., predawn Ψ of >–1.0 MPa) resulted in complete recovery of P_n after seedlings were rewatered. Other work with spruce species have also found that moderate drought had no effect on P_n after rewatering (Zwiazek and Blake 1989; Seiler and Cazell 1990; Johnsen 1993). However, as the severity of the drought stress increased, the ability of P_n to recover to prestress levels decreased. After a severe drought (i.e., predawn Ψ of <–2.0 MPa), P_n only reached 71% of predrought stress P_n after 14 days. Recovery of P_n immediately after relief from severe drought is related to the habitat preference and drought tolerance of a tree species (Pallardy et al. 1995). Spruce species seem to have the capability to quickly recover from moderate drought stress, although severe drought can cause a slow recovery of their gas exchange capability.

Growth is reduced when seedlings are exposed to low soil water (Section 2.1.3). Day and MacGillivray (1975) found that root growth ceased in newly transplanted white spruce seedlings at soil water below –0.6 MPa. In comparison to associated species (i.e., *Pinus*, *Populus*, *Betula*), spruce showed the greatest reduction in growth under moderate drought (Jarvis and Jarvis 1963*a*). Interior spruce seedlings exposed to water stress just after planting have reduced root growth (Fig. 3.5.2.1*e*). A continuous level of moderate water stress results in interior spruce seedlings having root growth reduction to 33% of optimum soil water, while a rapid severe or near-lethal drought prior to a period of optimum environmental conditions causes a 60 or 85% reduction in root growth, respectively. Thus, planting stress (Section 5.3) is exacerbated when spruce seedlings are planted into dry soils. These seedlings are under water stress and as a result are unable to generate the new root development needed to acquire sufficient soil water to relieve the water stress and resume growth.

Water stress can also influence the morphological development of spruce species throughout the growing season. The effects of continuous water stress on interior spruce seedlings across the growing season cause a 70–75% reduction in both shoot and root dry weights, while a rapid severe drought can cause a 20% reduction in shoot growth although has no effect on root growth (Fig. 3.5.2.1*f*). Drought stress during shoot elongation can reduce shoot growth (McClain and Armson 1975; Coutts 1982; Buxton et al. 1985; Roberts and Cannon 1992) as well as root growth (Coutts 1982; Feil et al. 1988; Seiler and Cazell 1990) in spruce seedlings, with the reduction in growth dependent upon the severity of stress. If the drought stress occurs during bud development, the terminal buds form fewer needle primordia (Fig. 3.5.2.1*f*), which has a direct bearing on shoot

Fig. 3.5.2.1*e*. Root growth of interior spruce seedlings ($N = 24$: mean + SE) after exposure to optimum (control), moderate drought, severe drought, or near-lethal drought. Drought treatments consisted of seedling exposure to the following conditions: moderate (M) drought (midday shoot Ψ of –1.0 to –1.5 MPa over the 25-day measurement period); severe (S) drought (midday shoot Ψ of –3.0 MPa and then grown under optimum soil water for 25 days); near-lethal (N.L.) drought (midday shoot Ψ of –4.0 MPa and then grown under optimum soil water for 25 days) (Grossnickle and Folk, unreported data).



growth in the next year (Section 2.6.1.1). These examples show how a moderate–continuous or severe–initial drought can limit spruce seedling growth, confirming work that has found that water stress in newly planted spruce seedlings on a reforestation site causes a subsequent reduction in seasonal shoot and root growth (Section 5.5.3).

Water use efficiency is an important component of the drought resistance strategy in plants. Water use efficiency is the ratio of carbon assimilated through photosynthesis in relation to the water lost through transpiration (Section 2.2.3). Water use efficiency can increase through a decrease in g_{wv}, which causes a proportionally greater decrease in transpiration than photosynthesis, or by an increase in photosynthesis. Studies on spruce species have found a positive relationship between increased water use efficiency (i.e., measured by $\delta^{13}C$) and increased dry matter production and greater photosynthesis (Flanagan and Johnsen 1995; Livingston et al. 1999) (Fig. 3.5.2.1*g*). Spruce species make a tradeoff between the maintenance of higher rates of carbon assimilation at the expense of greater water use. This may be due to the inherent characteristic that spruce species are naturally suited to forest sites having readily available soil water (Harlow and Harrar 1969), and may be one reason why spruce species perform better on reforestation sites with adequate soil water. In contrast, a larger proportional increase in water use efficiency occurs in pine, compared to spruce growing in dry habitats, indicating that pines are better suited to drier habitats and spruce to more mesic habitats (Carter and Smith 1988).

Fig. 3.5.2.1*f*. Seasonal (i.e., 12 weeks) morphological development of interior spruce seedlings ($N = 24$: mean + SE) after exposure to optimum soil water (control), moderate–continuous, or severe–initial drought. Drought treatments consisted of seedlings exposed to the following conditions: moderate–continuous (midday shoot Ψ of −1.0 to −1.5 MPa over the entire measurement period); severe–initial (midday shoot Ψ of −3.0 MPa and then grown under optimum soil water) (Grossnickle and Folk, unreported data).

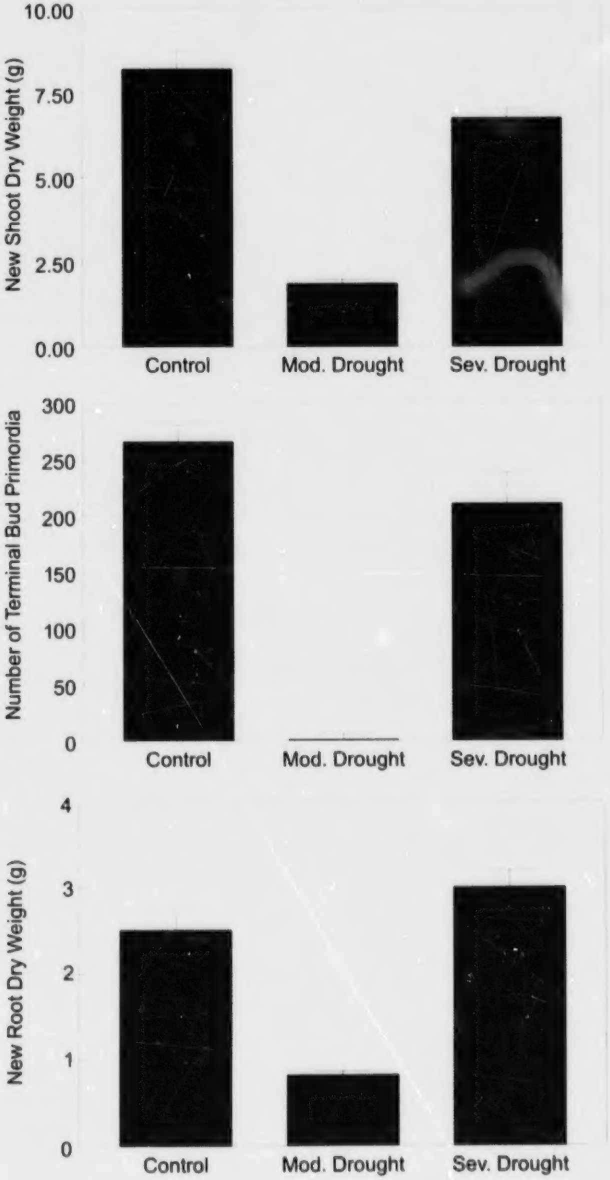
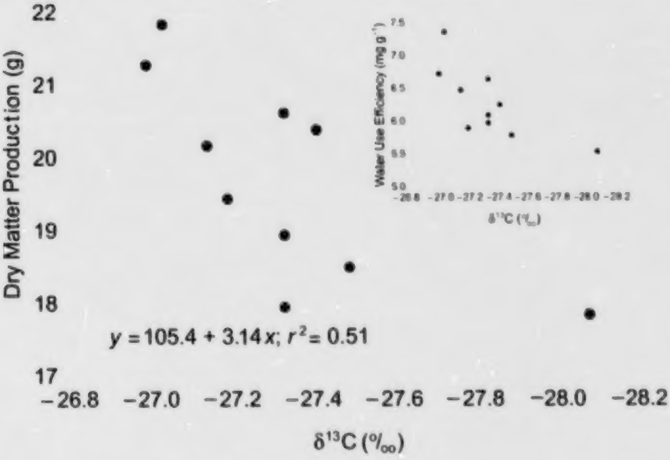


Fig. 3.5.2.1g. Carbon isotope abundance parameter ($\delta^{13}C$) versus dry matter production for 10 white spruce controlled crosses under dry land field conditions (adapted from Sun et al. 1996). Insert figure shows $\delta^{13}C$ versus long-term water use efficiency (i.e., ratio of dry matter production to the total water use for the growing season).



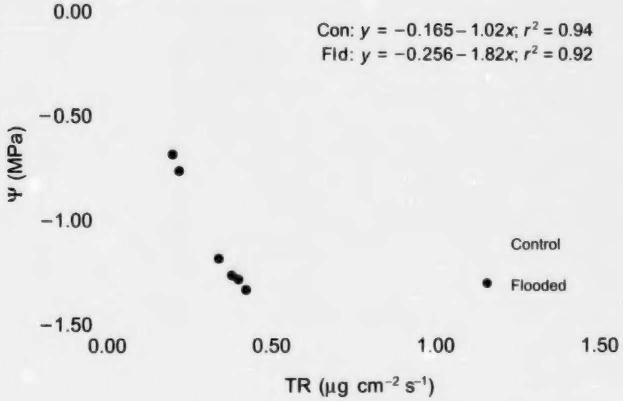
3.5.2.2 Excessive soil water

Plants vary considerably in their resistance to flooded soil (Kramer 1969; Lange et al. 1976). Flooding causes deficient aeration of the soil, with the level of this deficiency dependent on soil temperature and season. Dormant conifer species growing under low soil temperatures withstand the effects of flooding (Kozlowski 1982; Sutton 1991). For example, black and white spruce seedlings had little or no mortality when exposed to 28 days of flooding during an early spring thaw (Ahlgren and Hansen 1957). This indicates that both these spruce species can tolerate early growing season cold and flooded soils. However, extended flooding into late spring caused a marked decrease in the survival of white spruce, compared to nearly 100% survival of black spruce (Ahlgren and Hansen 1957). Varied tolerance to flooding occurs between black and white spruce during the initial stages of the growing season.

Under conditions of excessive soil water, total anoxia (lack of soil oxygen, Section 1.3.1) can occur in the soil. In this situation, plant tissues are unable to sustain metabolic processes. This is particularly critical for spruce species because they lack the ability to transport O_2, through the diffusion process, to roots under anaerobic soil conditions (Philipson and Coutts 1978; Conlin and Lieffers 1993). Spruce species need to be in nonflooded conditions during the growing season to regenerate new roots.

Under flooded soils, root systems are not efficient at taking up water to meet the seedling transpirational demands (Kozlowski 1982). For example, both black spruce (Grossnickle 1987) and white spruce (Fig. 3.5.2.2*a*) seedlings under flooded soil conditions have higher resistance to water movement through

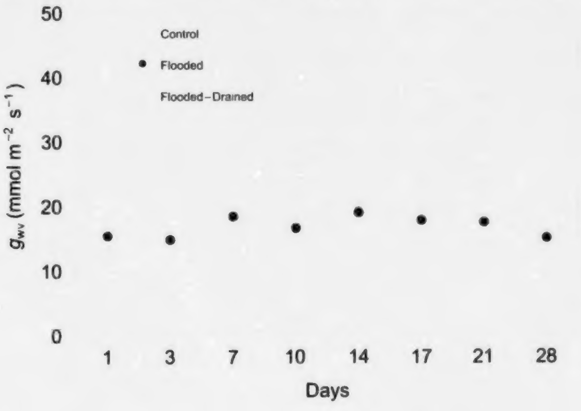
Fig. 3.5.2.2*a*. The relationship between transpiration rate (TR) and shoot water potential (Ψ) for control (Con) and flooded (Fld) white spruce seedlings (adapted from Grossnickle 1987).



the SPAC than nonflooded seedlings. A reduction in root system hydraulic conductivity is considered the cause for increased water stress in flooded spruce seedlings (Coutts 1981; Grossnickle 1987). A possible reason for this phenomenon is that anaerobic conditions resulting from flooding (Section 1.3.1) may damage the root xylem, which is contained by tyloses and (or) gum production (Zimmermann 1983). This containment of damaged root xylem reduces overall water flow through the xylem conducting pathway.

Flooding can cause stomatal closure and reduced P_n because poor aeration impedes water uptake by roots (noted above), causing a drying of needles (Kozlowski 1982). Black spruce seedlings planted into flooded soils showed reduced g_{wv} (Fig. 3.5.2.2*b*) and lower predawn Ψ (Grossnickle 1987). Black spruce also had reduced P_n under flooded soil conditions (Dang et al. 1991). After

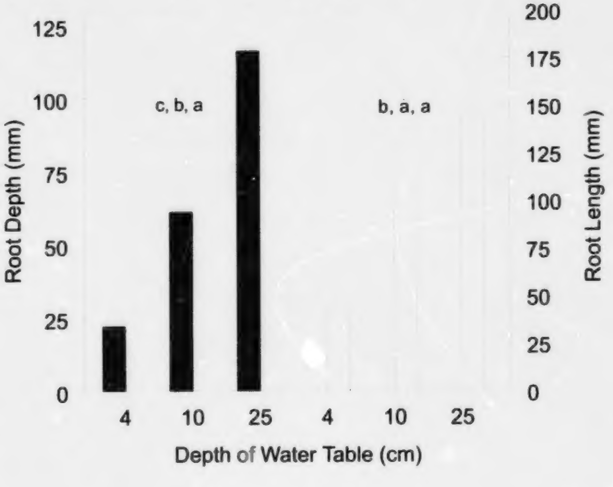
Fig. 3.5.2.2*b*. Needle conductance (g_{wv}) of recently planted frozen-stored black spruce seedlings in response to low soil temperature (10°C), optimum (control), flooded, or flooded and then drained soil conditions (adapted from Grossnickle 1987).



release from a 14-day flooding, black spruce seedlings required at least a 14-day period to recover normal gas exchange patterns (Fig. 3.5.2.2*a*), indicating the lasting effects of even short-term flooding on subsequent seedling performance.

Root regeneration in spruce species is inhibited by poor soil aeration, and this reduces growth (Zinkan et al. 1974; Levan and Riha 1986; Grossnickle 1987). Spruce species have limited root growth under flooded soils due to either their inability to initiate new roots or sustain root growth under flooded conditions. As the water table rises, seasonal root (Fig. 3.5.2.2*c*) and shoot (Lieffers and Rothwell 1986) growth declines in black spruce seedlings. If spruce seedlings are released from flooding, root growth resumes, albeit at much lower levels than seedlings that have not been flooded (Grossnickle 1987). Flooding during the spring thaw can cause a subsequent reduction in postflooding shoot growth of both black and white spruces (Ahlgren and Hansen 1957). Ahlgren and Hansen (1957) also found that needle damage was greater in white, compared to black, spruce, with greater needle damage occurring with an increasing number of days in flooded soils. Spruce species do not always recover from flooding. Flooding for 14 days caused high rates of mortality in actively growing white spruce seedlings (Lees 1964). Planting seedlings into saturated soils causes planting stress, thereby inhibiting root and shoot growth (Section 5.3).

Fig. 3.5.2.2*c*. Root development of black spruce seedlings grown in a soil system at 10°C root temperature with varying depths of the water table (adapted from Lieffers and Rothwell 1986). Bars with different letters (i.e., a, b, or c) are significantly different (nonparametric multiple comparison, $p < 0.05$).



3.6 Mineral nutrition

3.6.1 Nutrient uptake and internal mobilization

Planting spruce seedlings onto reforestation sites may place seedlings in direct competition with early successional species that have a greater capability for nutrient accumulation (Chapin 1983) (Section 5.5.4). Internal mobilization of nutrients and the external uptake of nutrients by spruce species also has an influence on their performance on nutrient-poor sites and on sites where there is competition for nutrients. Spruce seedling access to nutrients from the site and utilization of internal nutrient reserves have a direct bearing on long-term seedling development.

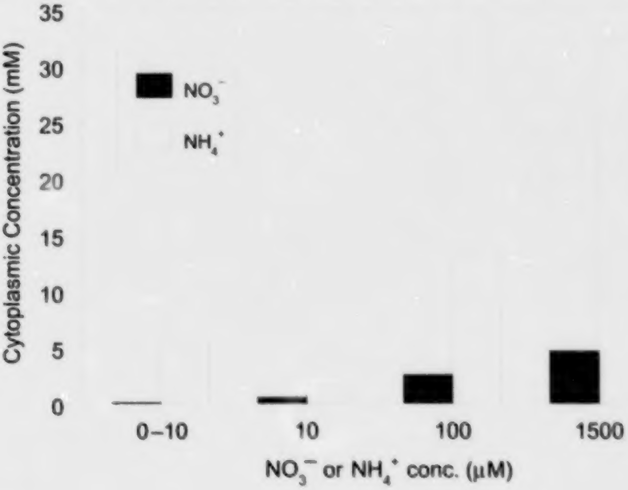
Nutrient uptake is tied to the site edaphic conditions. As stated previously, nutrients in the soil are supplied to the root surface of a seedling through the following mechanisms: (*i*) root growth, (*ii*) the mass flow of ions through the soil to the roots, and (*iii*) the diffusion of ions toward the root surface along a concentration gradient (Section 2.3.1). These factors interact with soil edaphic conditions to affect nutrient uptake by spruce species.

Soil water availability affects plant nutrient uptake from the soil in a number of different ways. The rate at which ions diffuse in soil solution to the root surface is related to the soil water content (the number of water-filled soil pores), and limited soil water reduces the number of water-filled soil pores (soil hydraulic conductivity, Section 1.3.1). Limited soil water also reduces the rate of transpiration (stomatal closure, Section 3.5.2.1), thereby restricting the flow of ions along with water in the transpirational stream. Lower soil water also causes a reduction in the permeability of roots to nutrients as well as water (Orem and Sheriff 1995). Water movement through spruce seedlings is also reduced under excessive soil water (Section 3.5.2.2). Root growth of spruce species is reduced under both limiting and excessive soil water (Section 3.5.2), which limits root contact with exchangeable nutrients. Numerous studies with agronomic species indicate that drought decreases nutrient uptake and concentration in plants (Viets 1972); recent work has shown this phenomenon to occur in Norway spruce (Nilsen 1995). The nutrient content of black spruce improved on sites that were originally flooded and then drained. This improved nutrient content was attributed to improved root growth, root metabolism, and site nutrient availability (Lieffers and McDonald 1990; MacDonald and Lieffers 1990). Nutrient acquisition is, therefore, constrained through limited root growth, plus the diffusion or mass flow of ions to the roots under conditions of both low and excessive soil water.

Nutrient uptake by spruce species can also be limited by low soil temperatures in a number of different ways. Water movement is reduced in spruce species under low soil temperature (Section 3.5.1), which limits the mass flow of ions to the roots. Spruce species also acquire nutrients through an active uptake process that requires energy, and low soil temperatures reduce the metabolic activity within spruce seedlings (Section 3.5.1). The acquisition of both N (Orem and Sheriff 1995) and P (Dighton and Harrison 1983) by spruce species decreases as soil temperature declines. The uptake of N by spruce roots at 5°C is only ~40% of the value at 20°C (Marschner et al. 1991), while P uptake by spruce roots stopped at 7°C because root metabolism was reduced (Dighton and Harrison 1983). Low soil temperatures limit spruce seedling nutrient acquisition through limited root growth, the diffusion or mass flow of ions to the roots, and the active uptake of nutrients through limited root metabolism.

The source of N available to spruce can influence nutrient uptake and utilization. Species indigenous to later successional forest habitats have been assumed to utilize NH_4^+ as their preferential nitrogen source (Smirnoff and Stewart 1985). In a recent series of studies on white spruce seedlings, NH_4^+ uptake was found to be substantially greater (up to 20 times greater) than NO_3^- (Kronzucker et al. 1995*a*, 1995*b*) (Fig. 3.6.1). Norway spruce also has a preferential uptake of NH_4^+ compared to NO_3^- (Marschner et al. 1991; Muller at al. 1996; Högberg et al. 1998). Norway spruce can utilize both nitrogen sources, although the rate of NH_4^+ uptake was much higher than that of NO_3^- when both sources were supplied (Ingestad 1979). A number of studies have found that NO_3^- can be an important source of N for Norway spruce forests, possibly due to the greater mobility of NO_3^- than NH_4^+ in soil solutions (Högberg et al. 1998; George et al. 1999). Interestingly, forest soils in mature forest ecosystems dominated by conifer species are generally considered to have a greater amount of NH_4^+, compared to NO_3^-, as an available nitrogen source, with the opposite condition on early successional disturbed sites (Smith et al. 1968; Klingensmith and Van Cleve 1993) (Section 1.5.2). This preferential N uptake pattern in spruce species can influence the accessibility of an adequate nitrogen source to spruce on a reforestation site.

Fig. 3.6.1. Difference in the accumulation of NH_4^+ compared to NO_3^- in the root cytoplasm of white spruce seedlings exposed to four external concentrations of the respective N sources (adapted from Kronzucker et al. 1995*b*).



Spruce species internally cycle nutrients on a seasonal basis, and this internal cycling is dependent on their yearly growth patterns. The over-winter storage of N (Millard and Proe 1992, 1993; Millard 1994; Proe and Millard 1994; McAlister and Timmer 1998; Malik and Timmer 1998), P (Proe and Millard 1995; McAlister and Timmer 1998), and K (McAlister and Timmer 1998) occurs in the stems, roots, and current-year needles of spruce seedlings. During the initial stages of growth in the spring, N and P are remobilized for new growth. This remobilization occurs for not only N and P but also K, resulting in the dilution of the existing internal nutrient pool as nutrients are allocated to expanding new shoots of black (Munson and Timmer 1990; Salonius and Beaton 1994; Malik and Timmer 1998) and white (Munson et al. 1995; McAlister and Timmer 1998) spruce seedlings. In Norway spruce shoots, 1-year-old needles served as the primary nutrient pool for young expanding needles, while 2- and 3-year-old needles contributed little to the retranslocation of ions (Weikert et al. 1989). The dilution process occurs for N, P, and K because these elements are easily redistributed from mature to young organs in all plants (Salisbury and Ross 1992).

Initial spring growth is dependent on the pool of nutrients taken up the previous year, but independent of the current nutrient supply in the soil. The required N (Millard and Proe 1992, 1993; Proe and Millard 1994; McAlister and Timmer 1998), P (Proe and Millard 1995; McAlister and Timmer 1998), and K (McAlister and Timmer 1998) needed for growth of spruce seedlings during the subsequent growing season was dependent on this remobilization process. Seedling total dry weight can more than double before the effects of nutrient availability from the field site start to influence seedling growth. This internal nutrient translocation phenomenon is the reason behind the use of nutrient loading as a nursery cultural practice to improve spruce seedling field performance on competitive sites (Sections 5.1.1.3 and 5.4.6.1).

Under conditions of N limitation on northern latitude reforestation sites, nutrient translocation was noted over 2 years in black spruce seedlings, with a continual situation of lower concentrations in older shoots than in currently growing shoots (Munson and Timmer 1990). The nutrient translocation process, under limited site nutrient availability, sometimes leads to chlorosis of the needles, due to N deficiency (Sections 2.3.3 and 2.6.1.4). This is a commonly seen phenomenon in spruce seedlings as they go through the establishment phase, and compete with early successional species, on reforestation sites (Section 5.5.4).

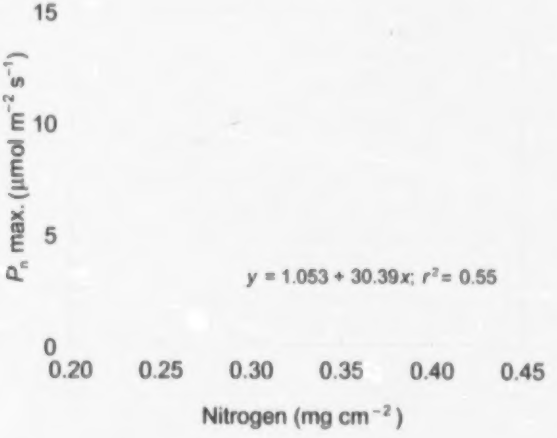
After shoot growth has ceased, plants continue the uptake of nutrients that are used for growth in the subsequent growing season. White spruce needles have an increase in nutrient content (N, P, K) during the late summer and early fall (Munson et al. 1995). Continued uptake of nutrients later into the growing season is required to accumulate the reserves that can then be stored in roots and current-year needles and mobilized during growth in the subsequent growing season.

3.6.2 Effect on physiological performance

Nutrient concentration of needle tissue has been related to many ecophysiological processes in conifer species. Greater nutrient concentration in conifer species has been attributed to improved gas exchange capability, drought resistance (i.e., avoidance and tolerance), freezing tolerance (reviewed by van den Driessche 1991*d*), and improved growth in the field (Section 5.4.6). This indicates the importance of adequate nutrient concentrations to maintain physiological activity and growth. Examples of the influence of nutrient content on the physiological performance of spruce species are discussed in the following section. Readers interested in detailed information on the importance of mineral nutrition for conifer seedling physiological activity and growth should consult van den Driessche (1991*a*).

The N concentration alters the P_n rate of spruce species. Shortages of N within the foliage reduce rates of P_n under conditions that are not otherwise limiting to plant growth. For many species, there is a strong positive relationship between P_n and increased leaf N concentration. Limitations in the availability of soil N and N-based compounds play a central role in regulating leaf CO_2 fixation capacity (Evans 1989). An increase in P_n with increasing needle N concentrations occurs in black (Johnsen 1993), Sitka (Chandler and Dale 1995; Brown et al. 1996*a*), Norway (Strand 1995, 1997) (Fig. 3.6.2*a*), red (Amundson et al. 1992), and white (Livingston et al. 1999) spruces. Norway spruce seedlings, fertilized with N, had faster recovery of photosynthesis from winter inhibition in the spring, compared with unfertilized seedlings (Strand and Lundmark 1995). In addition, a major portion of the seasonal variation of photosynthetic activity in

Fig. 3.6.2*a*. The relationship between light-saturated net photosynthesis (P_n) and N concentration for shoots of field-grown Norway spruce trees (adapted from Roberntz and Stockfors 1998). Note: P_n measurements were determined by one-sided needle surface area rather than total surface area, making P_n approximately four times those reported elsewhere.



newer needles of Norway spruce is associated with differences in needle N content (Strand 1997).

An increase in P_n with increasing N concentration is attributed to greater chlorophyll and carotenoid concentrations (Chandler and Dale 1995), thereby improving the light-harvesting activity (Centritto and Jarvis 1999) of photosynthesis. An increase in N concentration can also cause an improvement in the carboxylation capacity (i.e., dark reaction of the photosynthetic process) (Tan and Hogan 1995; Brown et al. 1996*a*; Centritto and Jarvis 1999). The increase in P_n with increasing N occurs in Sitka spruce as N moves from deficient to optimum concentrations, although P_n does not increase any further as N concentration moves into a region of luxury consumption (Chandler and Dale 1995; Brown et al. 1996*a*). Brown and associates (1996*a*) attributed the lack of P_n response at high N concentrations to self-shading as the shoots continued to develop.

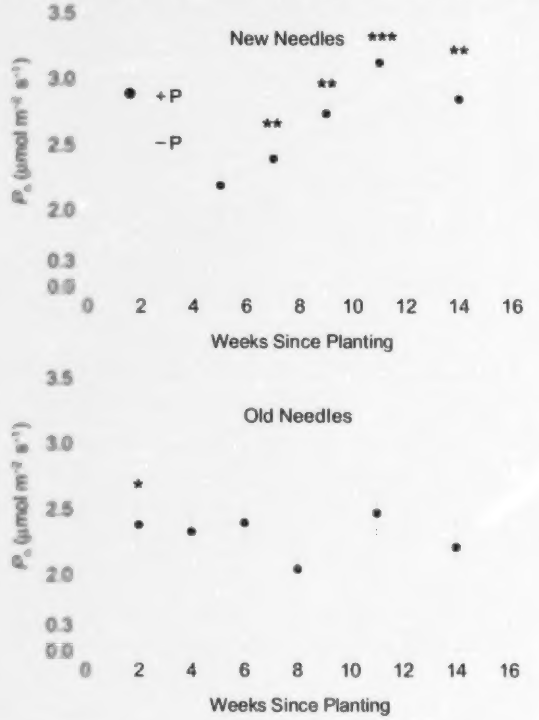
In some studies, g_{wv} of spruce increased with increasing N concentration (Chandler and Dale 1995; Roberntz and Stockfors 1998), resulting in fairly stable WUE patterns. Other work on conifer species has also found both P_n and transpiration to increase with increasing N concentration, resulting in very little change in WUE over a range of N concentrations (Mitchell and Hinckley 1993). In contrast, white spruce seedlings had a positive correlation between needle nitrogen content and $\delta^{13}C$ (i.e., improved WUE) that was likely associated with increased photosynthetic capacity at a greater N supply (Livingston et al. 1999).

During the fall, after spruce species have set bud, photosynthetic capacity declines with the decrease in seasonal temperatures (Section 3.3.1). Red spruce seedlings with high N content have a more rapid decline in P_n during the fall than seedlings with a low N content (L'Hirondelle et al. 1992). L'Hirondelle and associates (1992) believe that this response may be beneficial to the overall fall acclimation process of red spruce.

Little information is available on the effects of P on P_n for spruce species. In one of the few published examples, interior spruce showed no P_n limitation in response to P availability in older needles, yet in the same seedlings, P_n increased in newly formed needles in seedlings fertilized with P (Fig. 3.6.2*b*). Although no supporting information is available on the relationship of P_n to P for northern latitude species, work on other conifers has shown that P_n increases at greater leaf P concentrations (Sheriff et al. 1986; Rousseau and Reid 1990). As stated above, P is an element easily redistributed from older to younger needles. In this instance, P was redistributed to the newer foliage, causing a greater P_n in new shoots of seedlings fertilized with P. Increased P concentration in needles reduced the rate of g_{wv} in Sitka spruce seedlings and increased the sensitivity to increasing VPD (Bradbury and Malcolm 1977). This combination of increased P_n and decreased g_{wv} may lead to increased WUE in conifers having high P concentrations.

Respiration rates are also influenced by N and P content. In spruce species, maintenance respiration rates increase with N content (Ryan 1995; Strand 1997). Up to 50–60% of maintenance respiration supports the replacement and repair of proteins (Penning de Vries 1975), and in leaves, about 50% of this protein is

Fig. 3.6.2*b*. The rate of net photosynthesis (P_n) of interior spruce seedlings for old and newly developed needles during an optimum (controlled environment) growing season. Seedlings were supplied with an optimum nutrient regime with (+P) or without (–P) P. At times when the treatments were significantly different, P_n values were determined by an ANOVA and a Tukey's mean separation test at 0.10 (*), 0.05 (**), and 0.01 (***) p levels (Folk and Grossnickle 2000).



found in the chloroplasts (Salisbury and Ross 1992). Since N is a key component of all plant proteins (Table 2.3.3), it is logical that N content should be related to maintenance respiration as well as photosynthetic capacity. Increased stem respiration also occurs with increased N content in Norway spruce (Stockfors and Linder 1998), probably due to increased growth rates, a greater number of living cells in the stem tissue, and protein repair and turnover. Respiration rates also increase in Norway spruce with an increase in P nutrient content (Roberntz and Stockfors 1998). This phenomenon is attributed to P concentrations affecting a primary step (i.e., ADP phosphorylation) in the respiratory process (Amthor 1989).

Information on the effects of nutrient content on drought tolerance in conifer species is limited. Increased drought tolerance has been attributed to increased tissue content of K in Scots pine (*Pinus sylvestris* L.) but not in Norway spruce seedlings (Christersson 1[illegible]). The accumulation of K in chloroplasts allows P_n to continue at lower plant Ψ (Pier and Berkowitz 1987) and may be a mechanism promoting drought tolerance. Changes in drought tolerance can also be attributed to the influence of nutrient content on the phenological cycle of spruce species. Higher levels of nutrients can extend the duration of shoot and root growth in spruce seedlings (Section 3.6.3). Previous discussion has described how the drought tolerance of spruce species is at the lowest seasonal level during periods of shoot elongation (Section 2.1.1). Thus, an extended shoot growth period that results from increased nutrient content can keep spruce seedlings in the phenological stage where they are normally at a low level of drought tolerance.

Changes in freezing tolerance in response to nutrient content are difficult to interpret because the nutrient status of seedlings also alters their growth patterns and their phenological cycle. Any nutrient treatment that allows growth to continue and delays budset can delay the fall increase in freezing tolerance (Sections 3.7 and 3.9). However, increased nutrient addition can stimulate increased plant production of sugars, proteins, and fatty acids, compounds that contribute to the ability of plants to withstand freezing (Levitt 1980). Increased N in spruce seedlings that have already set bud increases freezing tolerance (e.g., Sitka: Benzian 1966; Norway: Pumpel et al. 1975; red: DeHayes et al. 1989, Klein et al. 1989, L'Hirondelle et al. 1992), while low N levels in spruce seedlings limit the development of freezing tolerance (Bigras et al. 1996). Interestingly, even though L'Hirondelle and associates (1992) found improved freezing tolerance in red spruce needles with high N content, this higher N content caused the buds to have a greater level of freezing damage. There was no real effect of P or K concentration on freezing tolerance of Norway spruce (Pumpel et al. 1975), while frost damage was reduced by the addition of P in Sitka spruce (Redfern and Cannell 1982). In contrast, Sitka spruce with lower N, P, or K content developed freezing tolerance more rapidly in the fall and early winter, with low-K trees having the greatest freezing tolerance (Jalkanen et al. 1998). Likewise, prior to budburst in the spring, the low-K trees still had the greatest freezing tolerance. Jalkanen and associates (1998) felt that nutrient deficiency, in this instance, increased freezing tolerance by limiting growth and increasing the availability of photosynthates to form cryoprotectants. The conflicting effects of nutrient content on the freezing tolerance of spruce species is probably dependent upon the interaction of their nutrient content and the phenological cycle.

3.6.3 Effect on morphological development

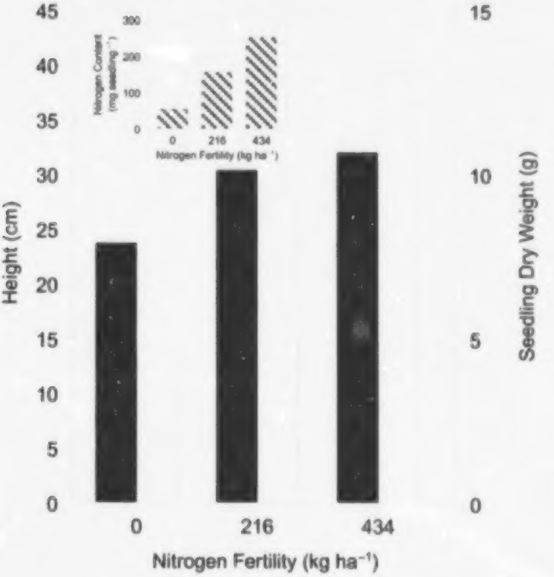
There is no simple or constant relationship between seedling growth and fertility, making it difficult to define standard patterns of spruce species response to fertility levels. The degree to which fertility influences seedling growth is also dependent upon what morphological parameters are being measured (e.g., height, diameter, roots). In this section, examples are presented to examine how the morphological development of spruce species changes in relation to N and P.

Increased N in spruce species normally increases growth (e.g., McClain and Armson 1976; Coutts and Philipson 1980; Brown and Higginbotham 1986; Millard and Proe 1992; L'Hirondelle et al. 1992; Mackie-Dawson et al. 1995;

Brown et al. 1996*b*). For example, white spruce seedlings fertilized with N had increased N content, with greater N content at higher fertilization rates (Fig. 3.6.3*a*). This indicated that the positive difference between the control and fertilization treatments can be regarded as N uptake resulting from the N treatments. After 3 years, the N treatments had increased N content by as much as 381%. Height growth and dry matter production had increased by up to 180% at higher N fertility. This example shows that increased N can stimulate spruce seedling growth.

Shoot growth patterns throughout the growing season can be altered by N levels. Altering N level affects the growth patterns for both white (McClain and Armson 1976) and Sitka spruce seedlings (Coutts and Philipson 1976, 1980; Brown and Higginbotham 1986; Millard and Proe 1992, 1993; Proe and Millard 1994). A high N level can result in two flushes of shoot growth during a single growing season. The first period of shoot flush occurs at a similar period of time for seedlings exposed to both high and low levels of N. The second period of shoot growth, for seedlings exposed to high N level, occurs in late summer. The high N level allows a continuation of free growth into late summer before bud induction. This second growth period occurs because there is further remobilization of N from shoots and roots. In addition, high N level can change the shoot structure by altering the arrangement of needles along the branches. High N level can reduce needle packing (i.e., fewer needles per stem unit length) (Skre and Nes 1996), with the greater needle internode lengths attributed to

Fig. 3.6.3*a*. Effects of N fertilization on nutrient content, height (filled pattern), and dry weight (open pattern) of white spruce seedlings after 3 years of growth in the nursery (adapted from McAlister and Timmer 1998).



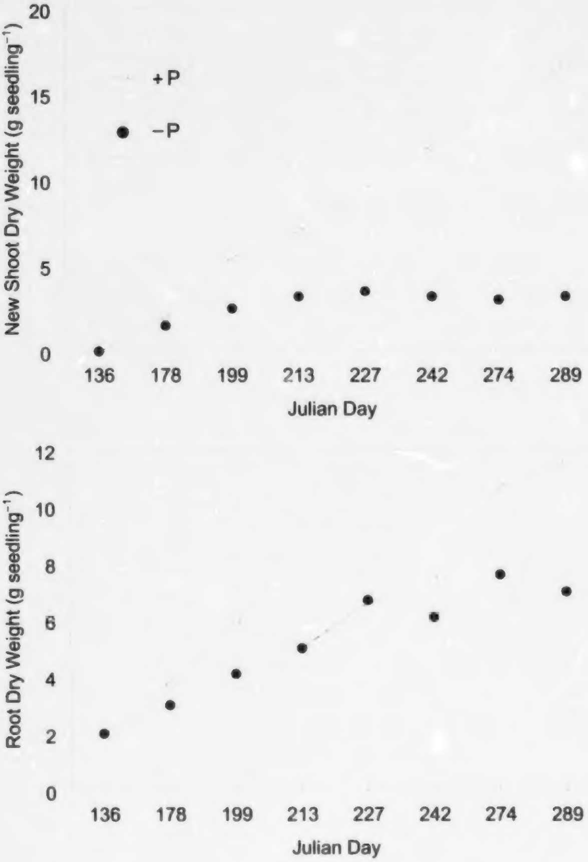
greater cell numbers rather than cell lengths (Section 2.6.1.3). Therefore, seedlings grown under high N level have greater overall shoot height, with needles spread out along the branches. At high N level, spruce seedlings set bud later in the fall (Murray et al. 1994), increasing seedling susceptibility to an early fall frost (Section 1.2.3). As a result, high, compared to low, levels of N not only increase total shoot biomass but also extend the length of time spruce species grow during the summer.

Spruce species increase root development with greater levels of N (McClain and Armson 1976; Coutts and Philipson 1976, 1980; Brown and Higginbotham 1986; Millard and Proe 1992, 1993; Mackie-Dawson et al. 1995; Brown et al. 1996*b*). Observation of in situ seasonal root growth patterns in Sitka spruce found a greater number of new roots on trees grown at higher N level. This high N condition caused a distinct seasonal bimodal root growth pattern which was related to trends in N uptake (Mackie-Dawson et al. 1995). In the late summer, Sitka spruce seedlings exposed to high N level also had greater root growth (Coutts and Philipson 1976), and continued root growth for a greater duration during the growing season (Coutts and Philipson 1980). Spruce species normally have a seasonal periodicity to root growth, with peaks usually occurring in early spring and fall (Section 2.6.2.1). Spruce species grown under high N level have greater root growth which results from greater growth during normal seasonal growth periods and from extension of the growing season.

Spruce seedlings grown under low N level have higher root to shoot ratios because a larger proportion of their total biomass is allocated to the roots (Coutts and Philipson 1980; Brown and Higginbotham 1986; Munson and Timmer 1990; Mackie-Dawson et al. 1995; Brown et al. 1996*b*). These higher root to shoot ratios under nutrient stress may represent a feedback mechanism by which reduced shoot growth and increased root growth increase nutrient uptake and nutrient status (Ingestad and Ågren 1988). However, decreased root to shoot ratio in Norway spruce was also associated with changes in root morphology, favoring shorter and thicker roots, with a reduction in total root system length (Seith et al. 1996). These root systems occupied less area within the soil system, which limited their capacity to take up nutrients. Greater root to shoot ratios at lower N can only enhance nutrient uptake if sufficient root development occurs into the soil system.

Altering the level of P can affect the growth pattern of spruce seedlings. For example, the growth of Sitka spruce seedlings was increased by the addition of P (Fig. 3.6.3*b*). This increased growth was reflected in both new shoot and root development. Low P concentrations also caused reduced shoot growth, compared to roots of Sitka spruce seedlings, increasing the root to shoot ratio (Proe and Millard 1995). In other studies, spruce seedlings that were not given adequate P had reduced total biomass during the growing season, when P became deficient (Armson and Sadreika 1979; Folk and Grossnickle 2000). Spruce seedlings that had adequate P upon entering the growing season showed no growth response to

Fig. 3.6.3*b*. Changes in new shoot dry weight and root dry weight during a growing season in either a +P or a –P treatment for Sitka spruce seedlings (Proe and Millard 1995).



subsequent P fertilization (Chapin et al. 1983; Folk and Grossnickle 2000). Reducing the availability of P during the growing season can limit the bud development of spruce seedlings (Chandler and Dale 1990; Folk and Grossnickle 2000). These examples show that P deficiencies can alter the biomass allocation and shoot growth patterns, and subsequently alter the morphological balance of spruce seedlings.

3.7 Freezing tolerance and dormancy

Boreal forests are located at latitudes where freezing temperatures can occur any time of the year (Section 1.2.1). As a result, spruce species are regularly exposed to air temperatures between 0 and –10°C during the growing season (Section 1.2.3), which can affect the performance of young plantations (Section

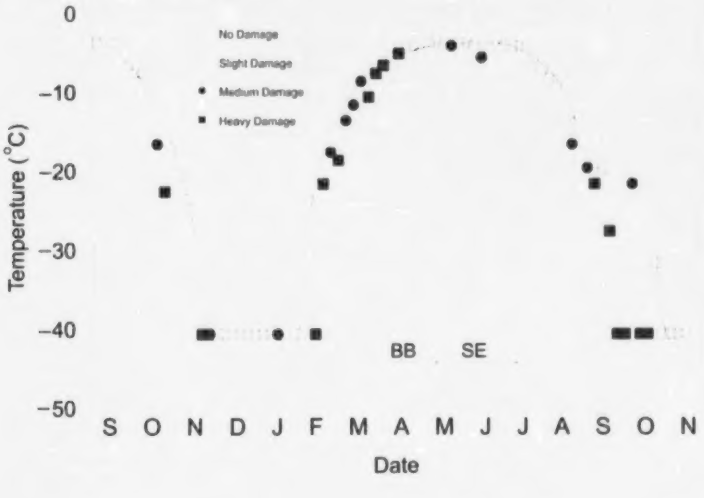
5.4.3). Reforestation sites can also have minimum air temperatures that regularly drop below –10°C starting in early fall. These freezing air temperatures can persist well into the spring (Section 1.2.1). During the middle of the winter, temperatures as low as –40°C occasionally occur. Spruce seedlings have to be capable of developing and maintaining freezing tolerance to withstand these freezing events that occur on northern latitude reforestation sites throughout the year.

3.7.1 Fall acclimation

Development of freezing tolerance in spruce species normally occurs in late summer and fall. An example of the seasonal cycle of freezing tolerance is shown for black spruce (Fig. 3.7.1*a*). This occurs as they become acclimated to seasonal changes in photoperiod (Section 1.1.4) and temperature (Fig. 1.2.1*a*) (Sakai and Larcher 1987). Freezing tolerance in spruce is induced by increased night length, although the development of freezing tolerance is greater and more rapid at lower temperatures (Aronsson 1975; Arnonsson et al. 1976; Christersson 1978; Silim and Lavender 1994).

The first stage of cold acclimation in conifers appears to result from exposure to the shortening days of late summer while air temperatures remain fairly warm (>10°C). In conifers, the cessation of shoot elongation and development of terminal buds indicates vegetative maturity (Burr 1990) and is considered the first stage of fall acclimation to low temperatures (Weiser 1970; Levitt 1980). Interestingly, free growth in young Sitka spruce did not increase the susceptibility to

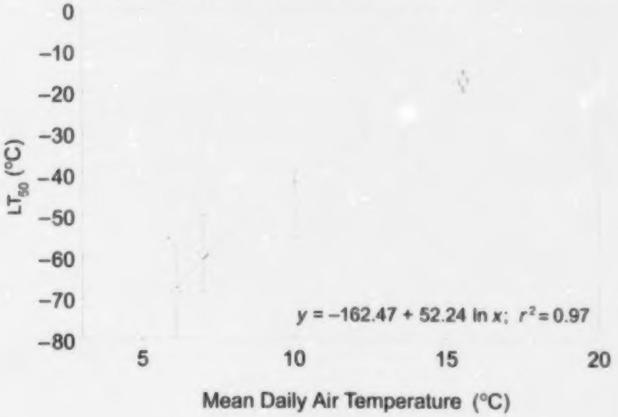
Fig. 3.7.1*a*. Seasonal pattern of freezing tolerance (i.e., defined by the temperature where a range of shoot tissue damage can occur) for black spruce over a 16-month period (adapted from Glerum 1973*a*). Shoot phenological stages are defined by (BB) budbreak and (SE) shoot elongation.



frost damage in the fall (Mboyi and Lee 1999), indicating that the timing of shoot growth cessation was more important than whether seasonal growth was due to either free or predetermined shoot growth (Section 2.6.1.1). After bud development, dormancy intensifies and freezing tolerance increases slightly (Burr 1990). Conifer species also use this period to accumulate stored reserves of substances to serve as an energy source for metabolic changes during the second stage of acclimation (Sakai and Larcher 1987). For Sitka (Cannell et al. 1990) and black (Glerum 1985) spruces, the initiation of freezing tolerance has been observed in the later stages of bud development when mitotic activity has decreased. For first-year black spruce, high levels of freezing tolerance do not usually develop until 4–6 weeks after bud initiation (Colombo et al. 1982). In contrast, Norway spruce appears to have a casual relationship between the cessation of mitotic activity and the development of freezing tolerance in the fall (Westin et al. 1999). During this late summer and early fall period, there is a cessation of shoot development and an initiation of freezing tolerance, although the exact sequence of events varies between spruce species.

The second stage of acclimation occurs when spruce species are exposed to low temperatures in early fall. When they reach maximum rest, freezing tolerance increases rapidly to a maximum (Burr 1990). For example, a rapid increase in freezing tolerance occurs in black (Fig. 3.7.1*a*), Engelmann (Burr et al. 1990), interior (Binnie et al. 1994) (Fig. 3.7.1*b*), Norway (Repo 1992), and white (Glerum 1973*a*; Bigras and D'Aoust 1993) spruces during the fall, as average air temperatures decrease. This rapid development in freezing tolerance enables spruce species to withstand freezing temperatures that occur in the fall (Section 1.2.1).

Fig. 3.7.1*b*. Relationship between freezing tolerance (determined by the freezing temperature resulting in 50% needle electrolyte leakage (LT_{50}); an indication of death of tissue) (mean ± SE) and mean daily air temperature in the fall for field-planted interior spruce seedlings (adapted from Grossnickle et al. 1996*a*).

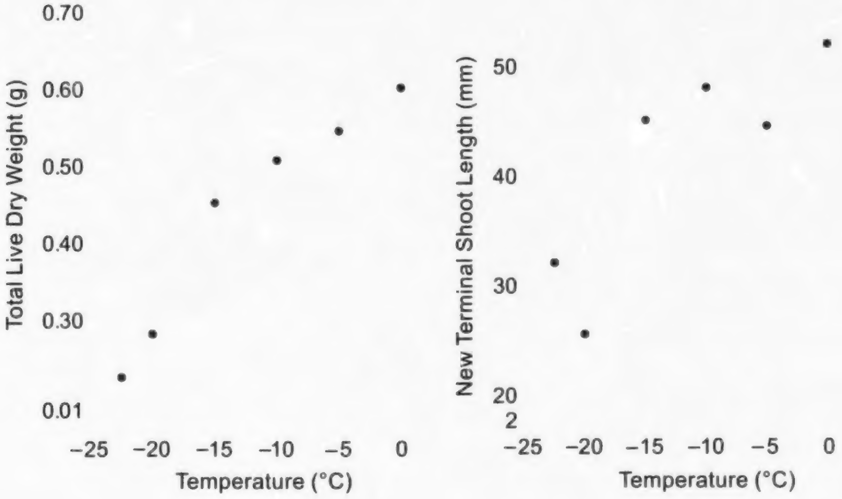


3.7.2 Winter patterns

Spruce species have high freezing tolerance during the winter. The shoot systems of spruce species that grow in the boreal forests can tolerate temperatures as low as –70°C (Sakai and Weiser 1973) (e.g., Fig. 3.7.1*b*) (Section 2.4); this level of freezing tolerance is far beyond the lowest winter temperatures (~–40°C) that are typically recorded during the winter in the boreal forests (Section 1.2.1). However, spruce species found in coastal (e.g., Sitka spruce) or more southern latitude lower elevation (e.g., red spruce) forests only develop freezing tolerance to temperatures as low as ~–40°C (Section 2.4).

Root systems of spruce species are not as tolerant to low freezing winter temperatures as their shoot systems. Root systems of spruce species have been reported to withstand temperatures only as low as –20 to –25°C (Havis 1976; Johnson and Havis 1977; Lindström 1986; Lindström and Nyström 1987). Fine roots of black spruce are not as hardy as woody roots (Colombo et al. 1995). Freezing damage to root systems can reduce spruce seedling establishment by reducing root growth (Colombo and Glerum 1984; Lindström and Nyström 1987) or shoot growth (Lindström and Nyström 1987; Bigras and Margolis 1997) during the subsequent growing season. For example, winter-hardened black spruce container-grown seedlings had increased damage to their root systems after exposure to freezing temperatures as low as –22.5°C, with a subsequent reduction in new shoot growth in seedlings with greater root damage (Fig. 3.7.2). Thus, care must be taken to avoid exposing seedling root systems to

Fig. 3.7.2. Relationship between the exposure of winter-hardened black spruce seedlings root systems to freezing temperatures and (*i*) total live root dry weight (live root dry weight determined 15 days after the freezing event); (*ii*) new terminal shoot length (assessed after 6 months under optimum environmental conditions) (adapted from Bigras 1997).



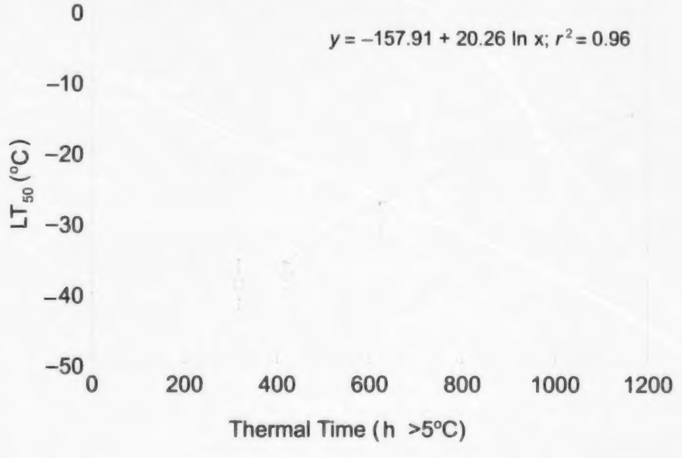
low air temperature extremes that can occur during the winter season in the boreal forest region.

Changes in the level of freezing tolerance in reaction to winter temperatures are attributed to the level of dormancy (Sakai and Larcher 1987). When spruce species are at the end of rest, freezing tolerance has reached a maximum (Glerum 1973*b*; Lavender 1985; Burr 1990). Early in winter, seedlings react more strongly to decreasing temperatures that increase freezing tolerance, while later in the winter and early spring (postdormancy stage), seedlings react more strongly to increasing temperatures that decrease freezing tolerance. For example, a 3-day midwinter thaw reduced freezing tolerance in red spruce (Strimbeck et al. 1995). The level of winter injury in red spruce increased with more numerous freeze–thaw cycles that occurred during the midwinter to late winter period (Lund and Livingston 1999). During midwinter, the short-term fluctuations in freezing tolerance of Norway spruce were correlated with changes in the daily minimum ambient temperature (Beuker et al. 1998). Spruce seedlings are susceptible to damage from sub-zero temperatures in late winter and early spring, after they have been temporarily exposed to warm temperatures (Krasowski et al. 1993*a*). These warm conditions cause freezing tolerance to decrease even before budbreak.

3.7.3 Spring deacclimation

As day length and temperatures increase in the spring, freezing tolerance decreases rapidly. At this stage, spruce species are at the end of rest, and warm temperatures allow them to break bud (Lavender 1985; Burr 1990) (Section 2.5). In certain northern latitude conifer species, a decrease in freezing tolerance

Fig. 3.7.3. Relationship between freezing tolerance (determined by the freezing temperature resulting in 50% needle electrolyte leakage (LT_{50})) ($N = 8$: mean ± SE) and thermal time (h >5°C) in the late winter and spring (prior to budbreak) for field-planted interior spruce seedlings (Grossnickle, unreported data).

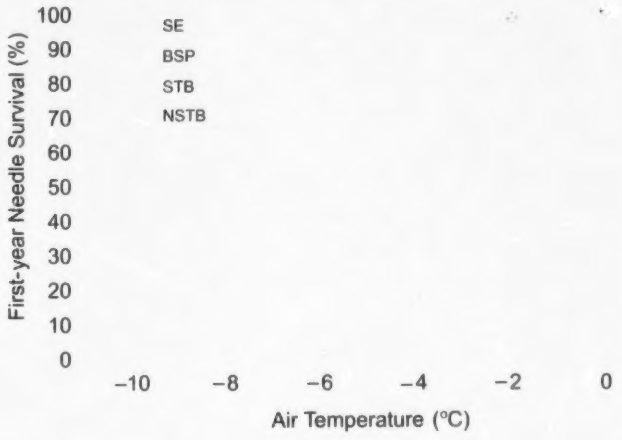


occurs before the buds begin to break, while other species retain considerable freezing tolerance as buds are flushing (Glerum 1973*a*, 1973*b*). Interestingly, black (Fig. 3.7.1*a*), Norway (Repo 1992), and Sitka (Sheppard and Cannell 1985) spruces all rapidly lose freezing tolerance prior to shoot growth in the spring, as field sites begin to warm. This decrease in freezing tolerance occurs as average late-winter air temperatures increase (Fig. 3.7.3). A number of spruce species also have a rapid loss of freezing tolerance in the spring, with the accumulation of thermal hours (i.e., h >5°C) (e.g., Norway: Aronsson 1975; Sitka: Cannell and Sheppard 1982). However, conifer species also detect when the photoperiod starts to increase (Section 1.1.4) and use this as a cue for dehardening (Greer et al. 1989). Due to this rapid loss of freezing tolerance, the buds of white spruce seedlings are damaged by frost just prior to flushing in the late spring (Clements et al. 1972).

3.7.4 Late-spring and summer frosts

During late spring and early summer, which are periods of shoot elongation, spruce species can withstand only very slight freezing temperatures. A typical spring and summer freezing tolerance pattern is represented by black spruce in Fig. 3.7.1*a*. Shoot damage during spring–summer freezing increases as temperatures decline to –10°C, even in black spruce seedlings, prior to any noticeable bud activity (Fig. 3.7.4). Greater damage occurs as buds begin to swell and then flush, and as new shoots elongate in black spruce. This pattern of loss in freezing tolerance in elongating shoots is typical of spruce species (Glerum 1973*a*; Christersson et al. 1987; Burr et al. 1990; Gillies and Binder 1997). For example, in Norway spruce, a temperature of –7°C caused little damage to swollen buds,

Fig. 3.7.4. Freezing tolerance (based on first-year needle survival after exposure to a range of freezing air temperatures) of black spruce seedlings during the springtime for (*i*) shoot elongation of 1–5 cm (SE), (*ii*) bud scales of terminal buds parting, with new needle tips emerging (BSP), (*iii*) swollen terminal buds (STB), and (*iv*) nonswollen terminal buds (NSTB) (adapted from Bigras and Herbert 1996).



while greater damage occurred at that same temperature as needles began to emerge from the bud scales (Dormling 1988), and elongating shoots were freezing tolerant to only −4°C (Repo 1992). Cannell and Sheppard (1982) found newly emerged Sitka spruce shoots could only tolerate temperatures of −5°C. Spruce seedlings have a very low level of freezing tolerance during shoot elongation and as a result are susceptible to summer frost that can occur on reforestation sites throughout the boreal forest (Sections 1.2.3 and 5.4.3).

The first visual signs of damage from a frost is a discoloration of needles. This results from a breakdown of chlorophyll, and as a consequence, there is a reduction in P_n (Section 3.3.1). Subsequent seasonal shoot growth of spruce seedlings is reduced if a damaging frost occurs just as the terminal bud shows signs of breaking (Clements et al. 1972; Bigras and Hébert 1996), or if the shoot has initiated elongation (Welander et al. 1994). Advection and radiation frosts occur on boreal reforestation sites during the growing season (Sections 1.2.3 and 5.4.3). As a result, spruce species can be exposed to freezing temperatures in the spring and summer that can cause injury, reduce physiological activity, and subsequently reduce growth (Section 3.3.1).

3.7.5 Winter desiccation

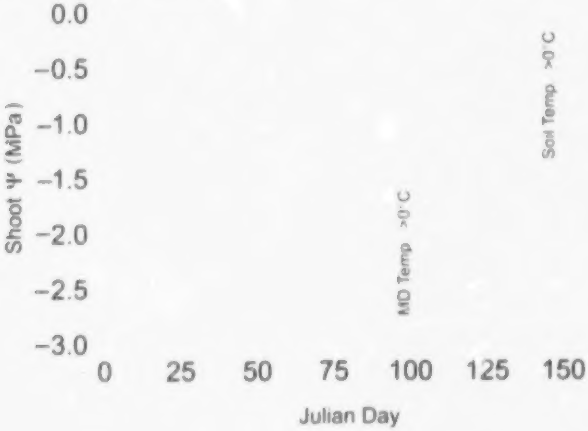
Shoot systems can be exposed to winter desiccation under conditions of frozen, snow-covered ground, bright sun, and dry air. This phenomenon is common in conifers (Sakai and Larcher 1987) and on boreal reforestation sites where snow does not consistently cover newly planted seedlings (Krasowski et al. 1993*a*). Injury from winter desiccation of spruce seedlings depends upon the depth to which the soil is frozen and the amount of the seedling shoot systems exposed above the snow cover to atmospheric conditions (i.e., air temperature, humidity, wind velocity).

Winter desiccation can occur in conifer seedlings when shoots are left exposed above the snow surface. Seedling shoots which are exposed to evaporative demand (i.e., VPD) of the air continue to transpire, although at low levels through partially open stomata and (or) from cuticular water loss (Sakai 1970). In general, cuticular transpiration in the winter for conifer species is less than 1% of summer transpiration, but this winter water loss is critical to a plant's winter water balance (Havranek and Tranquillini 1995). Needles on the windward side of Engelmann spruce trees had higher (i.e., more than twice) needle conductance than needles protected under snow cover, with needles from the leeward side of exposed shoots having intermediate values (Hadley and Smith 1983). Under these conditions, frozen water in the soil and conducting vessels of the stem restrict water flow through the SPAC pathway. As a result, water cannot be extracted from the soil, causing shoot Ψ to decrease typically to between −3.0 and −4.0 MPa during midwinter (Lindsay 1971). White spruce is defined as a species tolerant of winter desiccation because its stomata can remain partially open during the winter, causing shoot Ψ to decrease to as low as −4.0 MPa without injury (Cowling and Kedrowski 1980). It has previously been reported that conifer seedlings can tolerate severe drought at shoot Ψ values as low as –4.0 MPa, with death occurring at <–4.0 MPa (Section 2.1.3). Winter desiccation can sometimes become extreme enough to cause damage and possible tissue death due to lethal water stress (Tranquillini 1982).

Water stress in exposed spruce shoots is more common in the spring. Low springtime Ψ can occur as air temperature and evaporative demand increase, while the soil remains frozen (Cowling and Kedrowski 1980; Berg and Chapin 1994) (Fig. 3.7.5). In a similar vein, red spruce needles that reach low relative water contents have a higher degree of needle browning in early spring (Herrick and Friedland 1991; Hadley and Amundson 1992). Winter desiccation occurs with greater frequency in Norway spruce during late winter and early spring (Larcher 1985). It is also felt that severe winter desiccation in red spruce is often due to a prior freezing injury which damages the needles and allows for increased water loss (Strimbreck et al. 1991; Hadley et al. 1991; Hadley and Amundson 1992). Late winter and early spring are usually the time of the year when frozen soils limit water uptake required to meet the transpiration occurring as shoots are exposed to increasing evaporative demand of the air. Spruce species that are exposed to winter desiccation suffer needle browning and death in early spring.

Spruce species use a number of physiological mechanisms to avoid winter desiccation. Spruce shoots are able to absorb water directly through the woody stem (Section 2.1.2). This phenomenon can relieve winter desiccation because wet melting snow on the shoots can dramatically increase shoot Ψ of white spruce during late winter (Cowling and Kedrowski 1980). In addition, roots generally do not freeze until they reach temperatures between –1 and –3°C (Sakai

Fig. 3.7.5. Change in shoot water potential (Ψ) of black spruce throughout the winter and spring (Fairbanks, Alaska, 64°52′ N lat.) (adapted from Berg and Chapin 1994). Arrows indicate when mean daily (MD) air temperature and soil temperature at –15 cm were consistently above 0°C.



and Larcher 1987), which may allow roots to help relieve winter desiccation. Near-soil surface temperatures often remain near 0°C because of the high insulating qualities of snow (Section 1.2.1), which may allow low rates of water uptake to occur at soil temperatures near freezing (Section 3.5.1). In certain instances, the roots of Engelmann spruce saplings are able to take up small amounts of water during late winter and early spring through either deep unfrozen soil layers or from unfrozen pockets in the shallow soil layers (Boyce and Lucero 1999). These physiological mechanisms are ways spruce species can replenish their water reserves, even when the soil seems frozen, and relieve desiccation that can occur in late winter and early spring.

Another phenomenon related to winter desiccation is the abrasion of wax and cuticular layers of the needles. Winter desiccation of conifers can be exacerbated with exposure to wind (Tranquillini 1979). This occurs where shoots are exposed above the snow cover, and winds cause snow-blast conditions. Continuous abrasion by individual snow crystals can reduce the cuticle of Engelmann spruce needles, resulting in higher needle transpiration rates, caused by a substantial decrease in needle surface waxes (Hadley and Smith 1989). In addition, strong winds and needle abrasion can increase minimum needle conductance of Norway spruce needles (van Gardingen et al. 1991).

The development of needle surface waxes partly determine the level of winter desiccation avoidance provided to conifer needles (Hadley and Smith 1990). Spruce species with incomplete cuticular development during the growing season can have reduced resistance to cuticular transpiration during the winter (Larcher 1985). A number of studies have found greater winter minimum needle conductance in spruce collected from higher elevations (Baig and Tranquillini 1980; Tranquillini 1979; Herrick and Friedland 1991). Greater water loss through the cuticle has been attributed to a summer period too short for the production of an effective cuticle, although wind and snow damage to needle surfaces which originally possessed a fully developed cuticle or even stomatal disfunction cannot be discounted (Kerstiens 1996). Any combination of factors that result in higher water loss through the cuticle during the winter can cause the water content of the needles to fall below a critical level, which can result in winter desiccation damage.

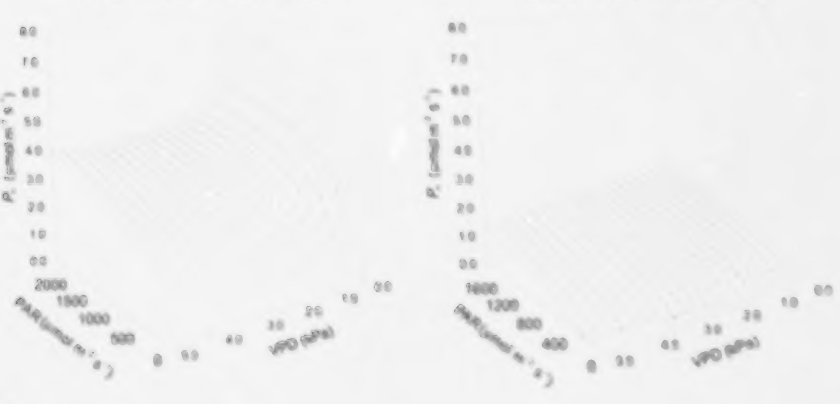
3.8 Response to multiple environmental variables

Seedlings can be exposed to a range of environmental conditions just after planting on reforestation sites, which can limit their performance. Major factors contributing to a limitation of seedling performance include the following edaphic factors: cold soil in the rooting zone, deficient soil aeration on wet sites, insufficient soil water on dry sites, and nutrient deficiency in the rooting zone. These edaphic stresses, coupled with dynamic changes in air temperature, evaporative demand, and light make it difficult to ascribe only one factor as limiting the physiological processes or growth of spruce seedlings. The following are examples wherein spruce seedling physiological response or morphological development in response to multiple environmental variables have been described. They provide an illustration of how the dynamic interaction of various environmental variables affects spruce seedling performance.

A combination of environmental variables can cause changes in gas exchange processes in spruce species. For example, gas exchange processes of interior spruce seedlings were primarily influenced by evaporative demand and light under optimum conditions of adequate soil water, soil temperatures between 15 and 20°C, and adequate fertility (Fig. 3.8*a*). In the field, however, light and VPD continually change in an interrelated fashion (Section 1.3.2). Thus, the relationship of P_n or g_{wv} to either light or VPD is not always easy to separate. It is sometimes better to examine the gas exchange process in relation to both of these atmospheric variables. For spruce seedlings, P_n increases as light increases. However, as VPD increases, P_n declines at all light intensities. This decrease in P_n as VPD increases (as air becomes drier) is attributed to a reduction in both g_{wv} and mesophyll photosynthetic processes (Schulze 1986).

When edaphic conditions are limiting, the gas exchange response of spruce species to atmospheric conditions is altered. Under reforestation site conditions exhibiting mild edaphic stress (i.e., seedlings had a midday Ψ of −1.2 to −1.4 MPa, soil temperatures ranged between 12 and 18°C, and fertility levels were low to moderate), the P_n response of interior spruce seedlings was generally similar to the pattern described for optimum edaphic conditions (P_n rising with increasing light and decreasing with increasing VPD) (Fig. 3.8*a*). However, P_n was reduced to 25% of those recorded under optimum conditions due to the moderately limiting edaphic conditions.

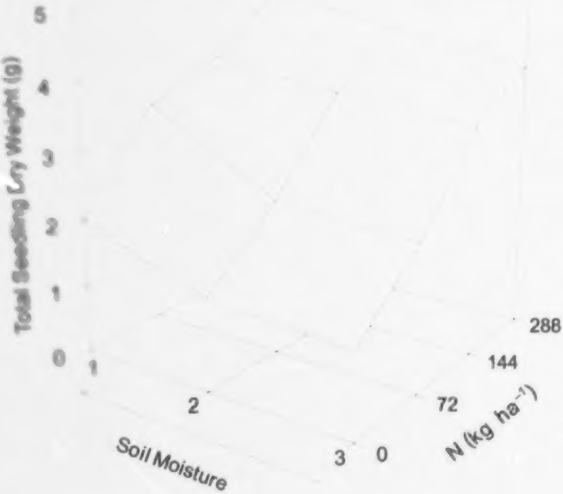
Fig. 3.8*a*. Net photosynthesis (P_n) of interior spruce seedlings in response to photosynthetically active radiation (PAR) and vapor pressure deficit (VPD) under either optimum or reforestation site edaphic conditions (optimum edaphic conditions adapted from Grossnickle and Fan 1998; reforestation site conditions adapted from Grossnickle and Major 1994*b*).



Variable edaphic conditions throughout the growing season can also influence the morphological development of spruce. For example, white spruce seedling growth response was altered, depending upon the combination of water and N fertility applied during the growing season (McClain and Armson 1976). Seedling growth was found to increase with increasing N fertility, and there was a marked response to a decrease in water, under a range of mild water stress (Fig. 3.8*b*). Mild water stress reduces growth of spruce species (Sections 2.1.3 and 3.5.2.1). McClain and Armson (1976) also found that seedling N concentrations increased with increasing N and decreasing water supplies; the higher N concentration at decreasing soil water content reflected a concentration of nutrients as seedling growth was reduced (Section 3.6.1). In a separate study, the interaction of increasing soil water content and fertility also significantly increased the dry weights of both black and white spruce seedlings (McClain and Armson 1975). These studies illustrate how spruce seedling growth response was altered under various combinations of water and fertility.

These examples illustrate how a combination of either optimal or limiting environmental conditions can alter the physiological performance and growth of spruce species. Generally, it is some combination of light, temperature, water, and nutrient supply that limits growth of woody plants (Mooney et al. 1991; Waring 1991; Larcher 1995). It is important to define the combination of reforestation site environmental conditions that limits successful seedling establishment (Gjerstad et al. 1984; Sutton 1985) and to implement silvicultural

Fig. 3.8*b*. Mean seedling dry weight of white spruce seedlings after two growing seasons in a bare-root nursery bed under the following soil water content and fertility combinations at a density of 215 seedlings m^{-2} (adapted from McClain and Armson 1976). Soil matric potential: (1) –0.025, (2) –0.05, and (3) –0.10 MPa. Nitrogen was applied every 3 weeks across the growing season at 0, 72, 144, and 288 kg h^{-1}.



practices that can enhance site environmental conditions required for improved seedling performance.

3.9 Response to seasonal cycles

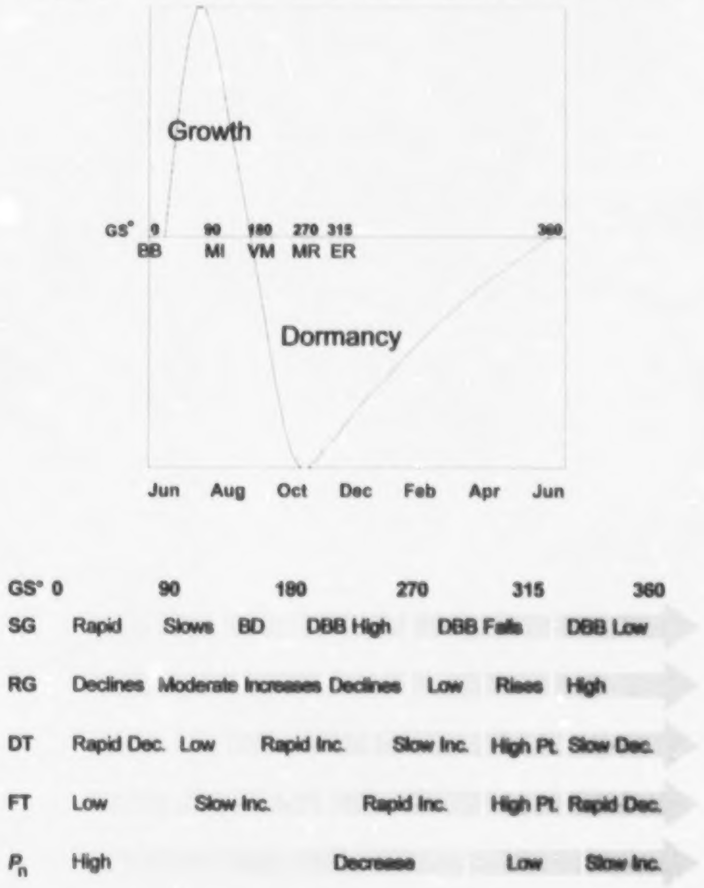
Spruce species undergo many morphological and physiological changes during an annual cycle in response to seasonal environmental conditions. The dynamic nature of these changes is illustrated by a degree growth stage model (Fuchigami et al. 1982; Fuchigami and Nee 1987). The degree growth stage model has been used by Burr (1990) and Ritchie and Tanaka (1990) to define the seasonal cycle of conifer species. Seasonal changes in phenological, physiological, and morphological parameters occur in parallel and are not always directly linked throughout the yearly cycle. As a result, sometimes these parameters do not follow typical seasonal trends when abnormal weather (e.g., Section 2.5) or nursery conditions (e.g., Section 5.1.3) affect varying cyclical patterns. Nevertheless, these general trends describe the dynamic pattern of seasonal change that occurs in spruce species.

A degree growth stage model of spruce species is intended to show the dynamic nature of their performance throughout the year. The model is presented to summarize growth, development, and physiological responses during a yearly cycle (Fig. 3.9). The growth stage model represents the annual cycle as a sine wave from 0 to 360°, with major degree growth stage (°GS) points estimated on the curve. Detailed descriptions of data on all of the parameters that are used to develop the growth stage model are described elsewhere in the treatise.

The 0–90°GS period is representative of mid to late spring through early summer. During this period, budbreak occurs in spruce species (Fig. 3.9). For a period of 4–8 weeks, seedlings are visibly active, with shoot elongation occurring (Fig. 2.6.1.1*a*). At the same time, the high root growth of the seedlings just prior to budbreak declines to a lower level (Fig. 2.6.2.1*b*). Due to this very active growth phase, photosynthetic levels of spruce species are at their highest seasonal level in order to provide the photosynthates needed for growth (Section 2.2.3). During this active phase, stress resistance of spruce species is at the lowest level of the year. Seedlings are very susceptible to extreme environmental conditions because they have a low level of both drought (Section 2.1.1) and freezing (Fig. 3.7.4) tolerance.

The 90–180°GS period is representative of mid- to late summer. Maturity induction (90°GS) is the point where plants first become responsive to day length (Fig. 3.9). This promotes the development of vegetative maturity (Fuchigami et al. 1982). During this period, shoot growth has slowed and terminal buds have been initiated. With conifers, the end of shoot elongation and development of over-winter terminal buds (Fig. 2.6.1.1*a*) is an indication of vegetative maturity (Burr 1990) and is considered the first stage of fall acclimation to low temperatures (Weiser 1970; Levitt 1980). At the same time, the root growth of spruce species increases (Fig. 2.6.2.1*b*). Photosynthesis of spruce species is maintained, as photosynthates are still needed for bud development and

Fig. 3.9. Degree growth stage model for spruce, depicting the seasonal cycle of morphological development and physiological processes. Abbreviations for the growth stage model are defined as follows: (BB) budbreak, (MI) maturity induction, (VM) vegetative maturity, (MR) maximum rest, (ER) end of rest. Abbreviations for morphological development are (SG) shoot growth, (BD) bud development, and (RG) root growth. Abbreviations for physiological processes are (DT) drought tolerance, (FT) freezing tolerance, and (P_n) net photosynthesis (compiled from Sections 2 and 3).



GS° 0 90 180 270 315 360

SG Rapid Slows BD DBB High DBB Falls DBB Low

RG Declines Moderate Increases Declines Low Rises High

DT Rapid Dec. Low Rapid Inc. Slow Inc. High Pt. Slow Dec.

FT Low Slow Inc. Rapid Inc. High Pt. Rapid Dec.

P_n High Decrease Low Slow Inc.

renewed root growth (Fig. 3.3.1*d*). During this phase, stress resistance of spruce species begins to increase, resulting in seedlings becoming more tolerant to drought (Section 2.1.1) and freezing (Fig. 3.7.1*a*).

The 180–270°GS period generally occurs in late summer and early fall. Theoretically, as dormancy intensifies from vegetative maturity at 180°GS to maximum rest at 270°GS, the number of days to budbreak (DBB) increases (Fuchigami et al. 1982; Burr 1990) (Fig. 3.9). After buds have fully formed, spruce seedlings develop what foresters call a "hard-bud," and mitotic activity within the bud declines to zero (Fig. 2.6.1.1*e*). This hard-bud does not break even if seedlings are exposed to optimal environmental conditions and long photoperiods (Fig. 2.5*c*). The capability of spruce species to grow roots declines to the lowest yearly level (Fig. 2.6.2.1*b*) and is indicative of this dormancy phase (Burr 1990; Ritchie and Tanaka 1990). Due to the further reduction in growth activity, there is less need for photosynthates, and photosynthesis of spruce species continues to decline (Fig. 3.3.1*d*). Stress resistance of spruce species continues to increase, resulting in seedlings becoming more tolerant to drought (Section 2.1.1) and freezing (Fig. 3.7.1*a*).

Maximum rest (270°GS) until the end of rest (315°GS) is a period characterized by an absence of shoot growth, a decrease in DBB to a low level, a rapid increase in freezing tolerance (Fuchigami et al. 1982; Burr 1990), an increase in drought tolerance (Grossnickle 1989; Colombo and Teng 1992) to a maximum level, and an increase in root growth capability (Burr 1990; Ritchie and Tanaka 1990). For spruce, this period typically occurs from early October through December (Fig. 3.9). During this period, DBB decreases to a low level (Fig. 2.5*c*), and root growth capability increases to the highest seasonal level (Fig. 2.6.2.1*b*). Both freezing (Fig. 3.7.1*a*) and drought (Section 2.1.1) tolerance increase rapidly in late October and November, and reach a maximum level by December. Photosynthetic activity is at a seasonal low level (Fig. 3.3.1*d*), which is also indicative of this dormancy phase (Binder and Fielder 1996*a*). Spruce species are at or near the end of rest (315°GS) by December.

From 315°GS, the end of rest, to 360°GS, when budbreak occurs, spruce species remain in what is called a quiescent state (Fuchigami et al. 1982; Burr 1990). During this period, spruce seedlings maintain a low DBB and a high root growth capability (Fig. 3.9). As day length and temperatures increase in the spring, freezing and drought tolerances begin to decrease (Fig. 3.7.3 and Section 2.1.1, respectively). Although growth has not started at this time, photosynthetic activity begins to increase and fluctuates, depending on air temperature (i.e., warmer air temperatures can cause an increase in P_n) (Fig. 3.3.1*d*). At this stage, seedlings are at the end of rest, and a period of warm temperatures is required for spruce species to break bud (Section 2.5) (Burr 1990). The decrease in stress tolerance begins before the buds begin to break. Thereafter, seedlings break bud, and the annual cycle of morphological development and physiological responses start anew.

4 Performance related to genetic variation

All species have an inherent range of physiological performance and morphological development traits, and these traits represent the genetic constitution of an organism. In addition, each species has a representative phenotypic response pattern arising from the reaction of these genetic traits to environmental stimulus. Spruce species have patterns of physiological response and morphological development in relation to site environmental conditions which are typical of the species genus (Sections 2 and 3). However, it is recognized that genetic variation exists both between and within northern spruce species. Examples of this genetic variation in ecophysiological performance are the focal point of this section.

In essence, there are two factors that increase variation: mutation and gene flow; and two forces that reduce variation: natural selection and genetic drift within a species (Wright 1976; Zobel and Talbert 1984). These factors and forces are at work to shape the genetic variation within and between species, including spruce species.

Mutations are heritable changes in the genetic makeup of a species, usually at a gene level. Most mutations that become fixed in a population are beneficial or neutral in their effects on a species. The beneficial mutations can contribute to adaptive genetic variation between and within species and populations, and they produce the variation that makes a species more adaptable to environmental conditions. Mutations that are deleterious in their effects on a species are removed from the population over time.

Gene flow is the migration of alleles from one population or one species into another where they are absent. When this transfer takes place between two species, it is called introgression. In northern latitude forest regions, closely related spruce species that occupy the same range can have introgressive hybridization. This may significantly influence genetic variation (Morgenstern 1996).

Natural selection is a process that generally reduces variability within a species because selection favors those trees with the genetic makeup best suited to grow in a given environment. Most northern spruce species are widely distributed throughout the northern latitude forests. Across these large species distribution ranges, there tends to be a pattern of subpopulations distributed along the environmental gradient. The term clinal variation is used to describe the gradient of genotypes within a continuous population. Clinal variation is the result of natural selection across a range of gradually changing environmental factors that correspond to changes in latitude and elevation. In northern latitude forests, clinal variation is common in widely distributed species (Morgenstern 1996).

Another type of natural selection can increase genetic variation within a species if two populations of the same species, exposed to different environments, become fixed over time for different alleles of a gene. This is called ecotypic variation and refers to a local population made up of genotypes adapted to a particular habitat because of natural selection within a local environment. It is felt that ecotypic variation occurs due to disruptive selection within populations where habitats are discontinuous and to stabilizing selection within subpopulations (Wright 1976; Zobel and Talbert 1984; Morgenstern 1996).

Genetic drift is a mechanism that occurs from chance fluctuations in allele frequencies within the progeny population compared to the genetic makeup of the parent population. Genetic drift tends toward reducing variation by fixing or losing alleles, and this is considered to have two important consequences (Wright 1976; Zobel and Talbert 1984; Morgenstern 1996). First, genetic drift reduces variation within subpopulations. Second, variation among subpopulations increases. The consequence of genetic drift is uniformity within the subpopulations that can increase susceptibility to extinction, for example, because of an inability to adapt to rapid changes in the environment.

Genetic variation within a species can have profound effects on the success of a silvicultural program. First and foremost, genetic variation can be used in tree breeding programs to provide improved seed sources. Improved seed sources can overcome a specific problem (e.g., insect or disease-resistant strains of trees), provide an enhanced product (e.g., improved wood quality, bole straightness, branch angle, or increased volume growth), or have the capability to respond to environmental conditions, associated with a given location, to ensure good growth. Tree breeding activities are incorporated into tree improvement programs where the control of tree parentage is combined with other silvicultural activities to increase stand productivity. Thus, tree improvement is a silvicultural activity that deals with the genetic makeup of trees used in forest plantations (Zobel and Talbert 1984). A seed orchard (i.e., a collection of individual trees selected for specific desirable traits within a defined seed zone) is the principle way in which seeds from tree improvement programs are currently produced for forest plantation programs. Vegetative propagation is also a silvicultural tool for producing plant material from a scarce seed supply, delivering genetic gains from selected families for improved traits or for clonal forestry. Vegetative propagation systems that are used to produce alternative spruce stock types that are not produced from seed are discussed elsewhere in this treatise (Section 5.1.4.3). Readers are referred to Wright (1976) and Zobel and Talbert (1984) for detailed discussions on the importance of tree improvement in plantation forestry programs.

There are also a number of reasons why it is important to understand the genetic variation that is inherent in the crop species planted onto the reforestation sites. These reasons deal with the deployment of seed sources and the expectations that foresters have when they integrate improved seed sources with silvicultural practices.

There needs to be careful consideration about the genetic source used to produce seedlings. It is essential that the genetic source selected for seedling production be ecologically suited to the field site environmental conditions throughout the entire forest rotation. Forest trees are wild plants with distinct geographic variation, and this genetic variation must be considered when planting seedlings across the forest landscape. Seed zones are geographic subdivisions of a species range based on genetic and ecological criteria (Lester et al. 1990; Morgenstern 1996). The parameters used to delineate seed zones for spruce species are elevation and geographic distance. The intent is to deploy well-adapted populations within defined geographic subdivisions of a species range. Seed zones are also designed to reduce the risk of transferring seed sources beyond their range of adaptation to regional environmental conditions and to limit the potential for long-term deleterious effects from genetic contamination at the new site. These seed zones provide a means of regulating how individual seedlots are collected and utilized for forest regeneration programs within defined geographic regions.

Foresters must recognize the capabilities as well as the limitations of silvicultural practices in shaping the forest environment where seedlings are to be planted. Silvicultural practices are very intensive within the forest regeneration aspect of a silvicultural program and can create microsites suited for seedling growth. However, the species and genetic sources used must be able to adapt to the local as well as regional environment, as silvicultural practices have only a limited effect on these conditions (Zobel and Talbert 1984; Morgenstern 1996). Therefore, the use of genetic material that is adapted to the local and regional environment is critical for the successful development of spruce plantations.

The genetic variation within a species is partly related to the long-term environment it is exposed to within its natural range. Diverse environmental conditions can cause natural selection to create genetic variation related to geographic origin. These diverse environmental conditions (i.e., light, humidity, temperature, and soil water and nutrition) are the same variables that affect the short-term physiological responses of a species to field site conditions. Thus, it is not surprising that a species displays genetic variation in its short-term physiological response and morphological development to a range of atmospheric and edaphic conditions. By defining this physiological response of a species to site environmental conditions, one provides a means to understand the biological basis for the adaptability of tree species to site (Dickmann 1992).

It is beyond the scope of this treatise to fully explore the genetic variation that is inherent within spruce species. Readers are referred to Morgenstern (1996) for a more in-depth discussion on the importance of applying the inherent genetic variation within a species towards improving silviculture programs.

Genetic variation in the performance of spruce can exist at a number of levels, and this variation can be used by foresters to improve survival and growth of forest plantations. The present section is intended to provide a series of examples of the range of genetic variation in the physiological response and morphological development of spruce seedlings to a range of environmental conditions. These examples are intended to illustrate the range of ecophysiological performance that can occur at the species, population, family, and clonal levels. Genetic differences detected in early years may often be expected to persist if related to adaptation in climatically diverse regions (Morgenstern 1996). The following examples of genetic variation in the ecophysiological response of spruce species are representative of long-term species performance traits.

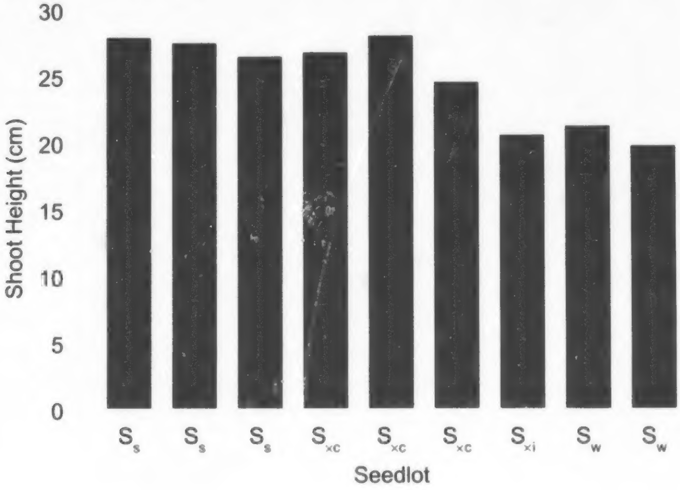
4.1 Introgression between interior and Sitka spruce

Introgression is defined as the limited spread of genetic material from one species into another species due to hybridization (Zobel and Talbert 1984). Introgressive hybridization takes place in northeastern North America where the ranges of black spruce and red spruce converge (Morgenstern 1996). The extent of hybridization for these spruce species across the landscape is related to the resemblance of intermediate sites between the parental site preferences of pure black and red spruces (Manley 1972). Another area is the Nass Skeena Transition, in British Columbia, where a large introgression zone occurs between Sitka, white, and Engelmann spruces (Little 1953; Daubenmire 1968; Roche 1969). Introgression occurs between interior spruce (i.e., the hybrid of Engelmann and white spruce) and Sitka spruce where populations of these two species coexist within the coast mountains of British Columbia. The mountains are a transition area between coastal and continental climatic conditions within British Columbia, and these conditions influence the gene pool of the Sitka × interior spruce hybrids within the region. Alleles from each of these three species have become incorporated into the gene pool of the other species within this introgression zone. Sitka spruce occurs naturally only in wet, maritime climates, while interior spruce occurs across continental areas which regularly have summer droughts and severe winters (Burns and Honkala 1990). Thus, species selection pressures within the introgression zone arise from frost and drought (favoring interior spruce) and competition for light on mesic sights (favoring Sitka spruce). These pressures are all important in the selection of well-adapted Sitka and interior spruce seedlots for reforestation. As a result, there are risks associated with using Sitka × interior seedlots from the Nass Skeena Transition area that have unknown genetic characterization.

The large introgression zone of Sitka and interior spruces in the Nass Skeena Transition area has been well investigated, and there have been a number of studies characterizing these spruce hybrids. Surveys of cone morphological characteristics delineated these spruce species (Roche 1969), with the mean free scale length and percentage free scale length of white spruce being smaller than those of Engelmann and Sitka spruces (Daubenmire 1968, 1974; Coates et al. 1994). Growth performance of Sitka spruce, interior spruce, and hybrids between the species have also been assessed in the nursery. Under optimum nursery conditions with an extended photoperiod, Sitka spruce seedlings became excessively tall, while interior spruce seedlings were much shorter, and hybrid seedlings were intermediate in height (Woods 1988) (Fig. 4.1*a*). This growth response is of major concern for forestry nurseries that are trying to produce Sitka and interior spruce seedlings with defined morphological specifications; hybrid seedlots of these species produce seedlings that have unpredictable morphological performance in the nursery.

Geneticists have long known that examining the DNA of plants can be an effective means of studying their genetic variation. Nuclear DNA, consisting of

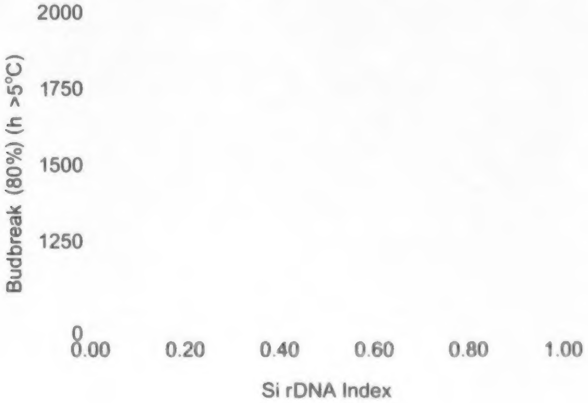
Fig. 4.1*a*. Seedling height growth of various Sitka spruce (S_s), coastal hybrid of Sitka and white spruce (S_{xc}), interior hybrid of Sitka and white spruce (S_{xi}), and white spruce (S_w) seedlots after being container-grown for 1 year in the nursery (adapted from Yeh and Arnott 1986).



two sets of chromosomes, is inherited equally from both parents. Thus, the nucleus contains a concentration of nuclear genes, half from the pollen parent and half from the seed parent. As a result, DNA probes can determine species contribution to the nuclear genomes of spruce hybrids (Sutton et al. 1994). The content of hybridization is estimated from an index based on the relative abundance of species specific polymorphic rDNA bands for each population. This analysis allows one to define the amount of Sitka × interior spruce hybridization within a seedlot based upon a quantifiable Si rDNA index value; a hybrid index ranging from zero (i.e., Sitka spruce) to one (i.e., interior spruce) (Sutton et al. 1994). A similar approach, developing an index using nuclear DNA markers, has been used to identify black spruce, red spruce, and hybrids of the two species (Bobola et al. 1996*a*, 1996*b*). This molecular genetics approach has been combined with ecophysiological characterization to provide a means to better define seedlots from the Sitka × interior spruce transition zone (Grossnickle et al. 1996*a*; Fan et al. 1997).

Flushing of terminal buds occurs as thermal time and daylight hours increase in spruce species (Section 2.5). There is a more rapid flushing of the terminal bud for seedlings from interior spruce (i.e., higher Si rDNA index) compared to Sitka spruce (i.e., lower Si rDNA index) populations (Fig. 4.1*b*). Sitka spruce populations required ~1900 h, while the hybrids required ~1600 h, of thermal time for 80% of their population to break bud. In contrast, interior spruce populations required 620 fewer hours of thermal time (i.e., ~1300 h) for 80% of their population to break bud.

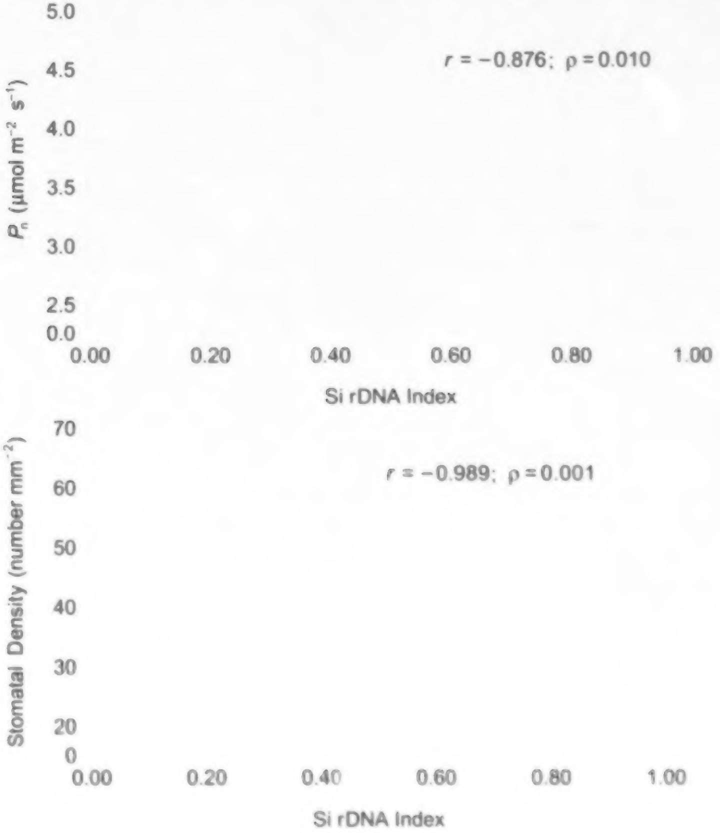
Fig. 4.1*b*. Number of thermal hours required for terminal budbreak (80%) of Sitka and interior spruce populations ($N = 120$) (defined by Si rDNA index). Si rDNA index of 0 = Sitka spruce, and Si rDNA index of 1 = interior spruce (Grossnickle, unreported data).



Northern or montane, compared to southern, ecotypes of conifer species begin the initiation of spring shoot growth after exposure to lower heat sums, or thermal units (Stern and Roche 1974). Spring temperatures control budbreak in black spruce with a gradual progression of earlier budbreak in sources that ranged from north to south (Morgenstern 1978). This phenomenon also occurs in white spruce (Coursolle et al. 1997) and Norway spruce (Heide 1974*b*; Dormling 1988). The difference in budbreak between Sitka and interior spruce could be the result of seasonal climatic conditions found within their native ranges. Continental locations, where interior spruce normally grows, are usually exposed to longer periods of low temperatures in the spring and a general decrease in the length of time when seasonal temperatures are optimal for growth of conifers. In contrast, maritime locations usually have warmer temperatures early in the spring and have a longer period when seasonal temperatures are optimal for growth of conifers. It would be advantageous for interior spruce seedlings to respond quickly to warm springtime conditions not only to take advantage of short growing seasons but also to delay budbreak for a period long enough to ensure that new shoots are not exposed to an early spring frost.

Differences in maximum P_n can occur between spruce species. For example, in the summer, under well-watered conditions, Sitka spruce populations had higher P_n than interior spruce populations (Fig. 4.1*c*). Greater P_n in Sitka spruce populations was not only due to greater photosynthetic efficiency at the biochemical level but partly due to anatomical differences between the two species (Fan et al. 1997). Sitka spruce populations had higher stomatal densities on their needles than the hybrids, while interior spruce populations had the lowest stomatal densities (Figs. 4.1*c* and 2.2.1*b*). These higher stomatal densities in Sitka spruce populations resulted in lower stomatal limitations to P_n. Recent

Fig. 4.1c. Net photosynthesis (P_n) (mean ± SE) of Sitka and interior spruce populations (defined by Si rDNA index) under well-watered conditions. Stomatal density (mean ± SE) of Sitka and interior spruce populations. Si rDNA index of 0 = Sitka spruce, and Si rDNA index of 1 = interior spruce (adapted from Fan et al. 1997).

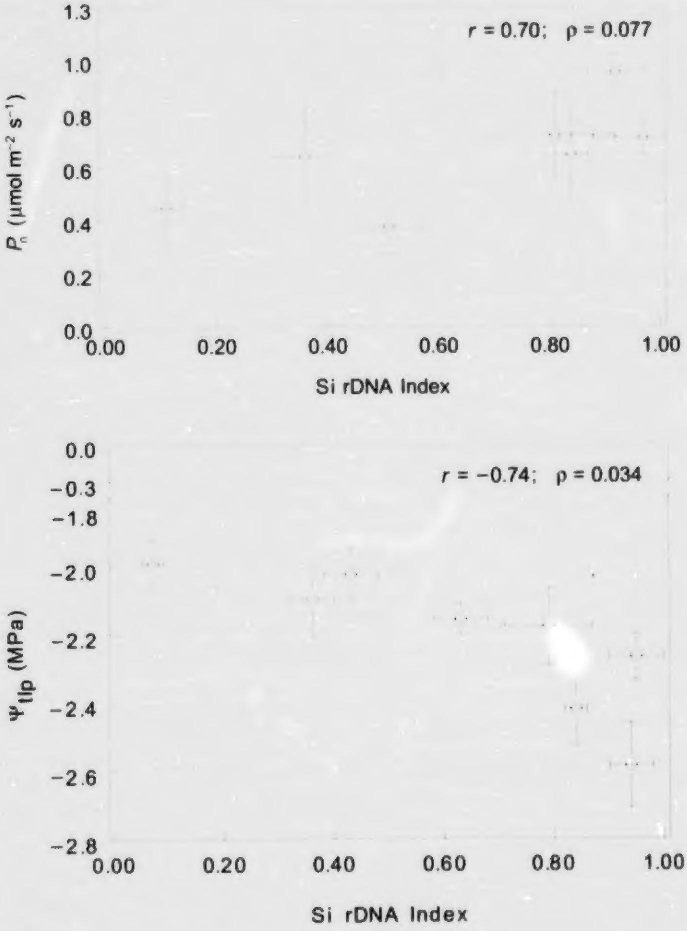


work has also found that Sitka spruce populations have higher long-term WUE than interior spruce populations under well-watered conditions (Fan et al. 1999). The higher WUE is attributed to the more efficient use of water by the Sitka spruce populations by having higher P_n levels in relation to the amount of water lost through transpiration (Section 2.2.3). This work indicates that under well-watered conditions Sitka spruce, compared to interior spruce, is more efficient at fixing carbon that is required for growth.

In work comparing black spruce, red spruce, and their hybrids, black spruce had greater P_n under low temperature conditions, while red spruce had higher P_n under warm temperature conditions (Manley and Ledig 1979). In contrast, hybrids of black and red spruces had at least 30% lower P_n than pure black or red spruce seedlings (Manley and Ledig 1979), while mature hybrid trees had comparable P_n rates to those measured on black spruce and red spruce trees (Johnsen et al. 1998). Manley and Ledig (1979) felt that these photosynthetic response differences were related to where black spruce and red spruce are found in the climax forest; black spruce is located in cold wet low-lying sites, while red spruce occurs in warmer well-drained uplands.

Just after the summer shoot growth period, spruce species develop greater levels of drought tolerance (Section 2.1.1). During this period, summer drought tolerance (Ψ_{tlp}) was greater in interior spruce populations than Sitka spruce or hybrid populations (Fig. 4.1*d*). This species specific drought tolerance pattern

Fig. 4.1*d*. Net photosynthesis (P_n) (mean ± SE) of Sitka and interior spruce populations (defined by Si rDNA index) under soil drought (adapted from Fan et al. 1997). Drought tolerance (osmotic potential at turgor loss point: Ψ_{tlp}) (mean ± SE) of Sitka and interior spruce populations just after summer budset (adapted from Grossnickle et al. 1996*a*). Si rDNA index of 0 = Sitka spruce, and Si rDNA index of 1 = interior spruce.

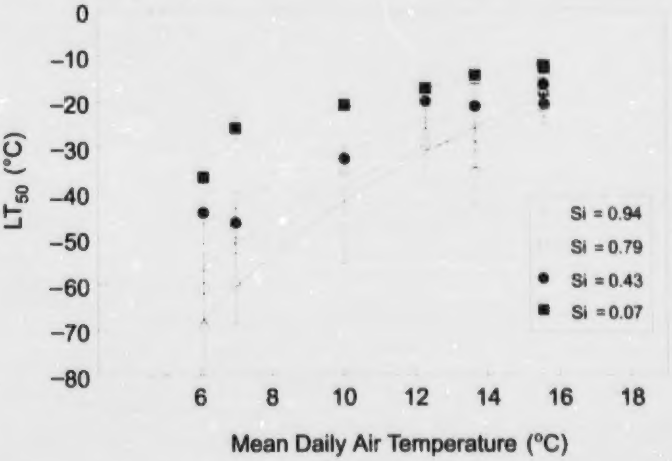


was consistent throughout the year (Grossnickle et al. 1996*a*). Under summer drought, all populations had suppressed gas exchange capacity, with interior spruce populations having greater gas exchange capacity (Fig. 4.1*d*). Greater osmotic adjustment and gas exchange capacity under drought are parts of the drought tolerance strategy inherent in spruce species (Section 3.5.2.1). Findings indicate that interior spruce, compared to Sitka spruce, are better able to tolerate drought and continue to photosynthesize under limiting soil water conditions.

The development of freezing tolerance occurs in spruce species when they are exposed to low fall temperatures (Section 3.7.1). Differences in freezing tolerance between spruce populations became greater as the mean daily air temperature declined in the fall, with Sitka spruce populations having the least and interior spruce populations having the greatest freezing tolerance throughout fall acclimation (Fig. 4.1*e*). This agrees with work showing that Sitka spruce, compared to Engelmann and (or) white, has a slower development of freezing tolerance in the fall (Sheppard and Cannell 1985; Kolotelo 1991) and a lower survival rate in severe winter conditions (Ying and Morgenstern 1982). At most measurement times, hybrids of the Sitka × interior spruce complex have intermediate levels of freezing tolerance when compared to Sitka and interior spruce populations (Fig. 4.1*e*), which are similar to other reported work on this spruce complex (Ying and Morgenstern 1982; Sheppard and Cannell 1985; Kolotelo 1991).

These results indicate that Sitka × interior hybrid populations have identifiable ecophysiological patterns. Application of this information ensures that restocking failures do not occur due to frost, drought, or growth rate because of

Fig. 4.1*e*. Fall changes in freezing tolerance (defined by LT_{50}, the freezing temperature resulting in 50% needle electrolyte leakage) (mean ± SE) in relation to mean daily air temperature from four Sitka × interior spruce populations. Si rDNA index of 0 = Sitka spruce, and Si rDNA index of 1 = interior spruce (adapted from Grossnickle et al. 1996*a*).



improper placement of Sitka × interior spruce seedlots. Currently, this information is being used to characterize seedlots found within the Nass Skeena Transition zone in British Columbia (Grossnickle et al. 1997). This provides for wise deployment of Sitka × interior hybrid seedlings onto reforestation sites.

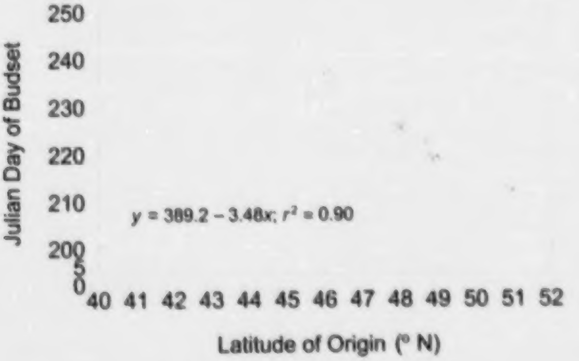
4.2 Genetic variation between populations during fall acclimation

Populations of a spruce species consist of individuals occupying particular geographic regions to which they are adapted. Spruce species exhibit clinal variation, a gradient of genotypes within the continuous spruce population due to natural selection for changing environmental conditions (in this case temperature) that correspond to changes in latitude and altitude. Changes in photoperiod length are an indirect cue for northern spruce species to recognize that environmental conditions are about to change. Characteristics that reflect differences between populations can be both phenological and physiological in nature and can be used to define population differences within a species for resistance to cold temperatures (Zobel and Talbert 1984).

Bud development of spruce species is triggered primarily by the shortening in the length of the photoperiod as summer progresses (Section 2.5). The photoperiod at which spruce seedlings set bud in late summer is related to both latitude and elevation of origin.

The following examples describe the relationship between photoperiod at which spruce species set bud based on latitude of origin. Black spruce from more northerly latitudes set bud earlier during the growing season than more southerly sources (Fig. 4.2*a*) (Johnsen and Seiler 1996). Critical photoperiods for Sitka spruce can range from as low as 9 h for southern sources (~45° N lat.) to 14 h for northern sources (~58° N lat.) (Pollard et al. 1975). Cannell and Willet (1975) also studied Sitka spruce and found that bud development was completed at longer photoperiods in sources from more northern latitudes. Some northern latitude sources of Norway spruce can have critical photoperiods as long as 21 h

Fig. 4.2*a*. Date of terminal budset in black spruce seedlings, grown in the same location, for populations collected from a range of latitudes (adapted from Morgenstern 1976).



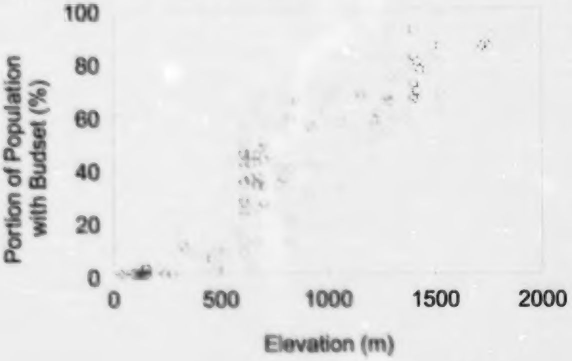
(64° N lat.) (Heide 1974*a*) to 18 h (60° N lat.) (Dormling et al. 1968), with the length of photoperiod declining for more southern sources (i.e., 15 h (47° N lat.) (Heide 1974*a*)). In contrast, white spruce populations from ~44 to 46° N lat., and similar elevation, all had a critical photoperiod of around 13 h (Pollard and Ying 1979*a*).

The photoperiod at which spruce species set bud in late summer is also related to elevation of origin. Roche (1969) found that seedlings from seed sources collected at high elevations completed shoot development at a longer photoperiod than seedlings from low-elevation seed sources (Fig. 4.2*b*). This same pattern was evident for Sitka (Campbell et al. 1989) or Norway (Heide 1974*a*) spruce populations from across a range of elevations at the same latitude. Findings from all of these studies point to the fact that photoperiod is one of the mechanisms that regulates budset in spruce species. The general statement can be made that spruce species from northern latitude seed sources set bud at longer photoperiods than spruce seedlings from southern latitude seed sources and that this trend is paralleled by an elevational sequence in mountainous regions where seed sources from higher elevations set bud at longer photoperiods than spruce seedlings from low-elevation seed sources.

Even though bud development of spruce species is triggered primarily by the shortening in length of the photoperiod as summer progresses, this stimuli may be modified by decreasing temperatures (Section 2.5). For example, in Sitka spruce, the influence of temperature on cessation of growth and bud development is stronger in southern than northern populations (Malcolm and Pymer 1975). It is this combination of day length and decreasing temperatures that triggers bud development of various genetic sources in spruce species during the fall.

After budset, needle initiation of spruce species follows a rapid phase of development for a period of up to 6 weeks, with the number of needle primordia formed dependent upon environmental conditions during this developmental phase (Section 2.6.1.1). Interestingly, fast-growing, compared to slow-growing, white spruce populations were able to extend the period of rapid needle initiation

Fig. 4.2*b*. Percent terminal budset of spruce populations on Julian day 164 collected from a range of elevations and grown in the same location (adapted from Roche 1969).

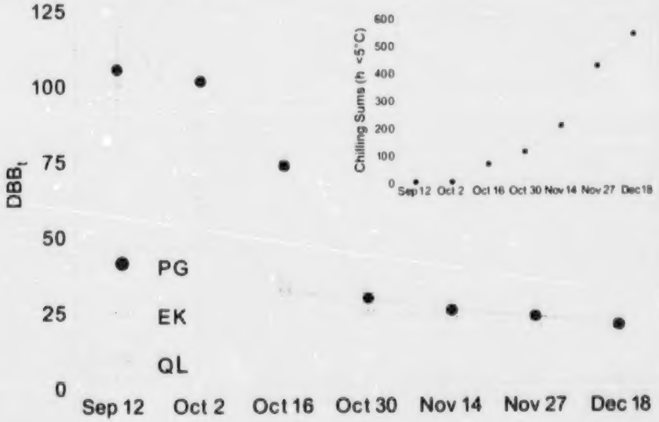


further into the fall (Pollard 1973). These differences reported by Pollard (1973) were not attributable to latitude of seed source origin, although Burley (1966) noted southern sources of Sitka spruce formed needle primordia throughout the fall, while northern sources stopped development in early fall. Northern, compared to southern, populations of Sitka spruce developed needle primordia at a more rapid rate during the initial period of bud development, while southern populations continued development later into the fall (Pollard et al. 1975). These studies indicate that there is a degree of inherent variability in the speed with which needle primordia develop in the buds of spruce species.

After spruce seedlings have formed fully developed terminal buds on their shoots in late summer, they are considered dormant. This dormancy can only be reversed if seedlings are exposed to a series of environmental cues that move them through the various dormancy phases. The main environmental cue is temperature (Section 2.5), as spruce populations have a specific chilling requirement.

The following is an example of the fall acclimation pattern of interior spruce at the population level. As the number of chilling hours (h <5°C) increased, the days required for terminal budbreak (DBB_t) decreased for all seed sources in a manner that is typical for interior spruce seedlings moving towards the end of rest (Section 3.9). The rate of DBB_t decrease was related to seed source, with the southernmost source (East Kootenay) having the most rapid decrease in DBB_t, and the northern seed source (Prince George) having the slowest decrease in DBB_t (Fig. 4.2*c*). However, by late October, all seed sources had a similar rate of DBB_t, and this continued through the rest of the fall. The more northern seed sources required a greater number of chilling hours to reach the end of rest and achieve a quiescent state of dormancy.

Fig. 4.2*c*. Days to terminal budbreak (DBB_t) (mean ± SE) of interior spruce seedlings from East Kootenay (EK; 50° N lat.), Prince George (PG; 53°22′ N lat.), and Quesnel Lake (QL; 53°13′ N lat.) seedlots. Inset figure shows the chilling sum as accumulated hours (adapted from Binnie et al. 1994).



Spruce species have a seasonal fall decline in their photosynthetic capacity (Section 3.3.1). This fall decline in P_n is directly attributable to a decline in both air and soil temperatures and is indirectly due to the dormant state of seedlings which reduces their demand for photosynthates that are required for growth. Interestingly, southern black spruce populations that grew later into the fall also displayed higher P_n throughout the fall than seedlings from northern populations (Fig. 4.2*d*). Johnsen and associates (1996) attribute this late-season P_n activity in the southern populations to continued needle primordia development that would have a demand for photosynthates, thus higher late-fall P_n. Norway spruce (Tranquillini and Havranek 1985) and white spruce (Binder and Fielder 1996*a*) populations also showed northern, compared to southern, latitude populations had a more rapid decrease in their photosynthetic capacity in response to the decline in fall photoperiods and temperatures.

Development of freezing tolerance in spruce seedlings normally begins with the seasonal changes in photoperiod and temperature that occur in late summer, after shoot growth has ceased, buds have formed, and the dormancy process has begun (Section 3.7). During the fall, the freezing tolerance level for all seed sources increased in a manner that is typical for spruce seedlings undergoing fall acclimation (Fig. 4.2*e*). The rate of increase in freezing tolerance was related to seed source, with the southernmost source (East Kootenay) having the slowest rate and both of the more northern seed sources (Prince George and Quesnel) having a faster rate. By early December, the southernmost seed source had the least development of freezing tolerance compared to the more northern seed sources. This pattern is typical of white and interior spruce seed sources, with

Fig. 4.2*d*. Fall progression of net photosynthesis (P_n) (mean + SE) of four diverse populations of black spruce from a field provenance test located at the Petawawa National Forestry Institute, Ontario (46° N lat.) (adapted from Johnsen et al. 1996). Statistical significance from an ANOVA, by date, is indicated with $* = p \le 0.1$ and $*** = p \le 0.01$.

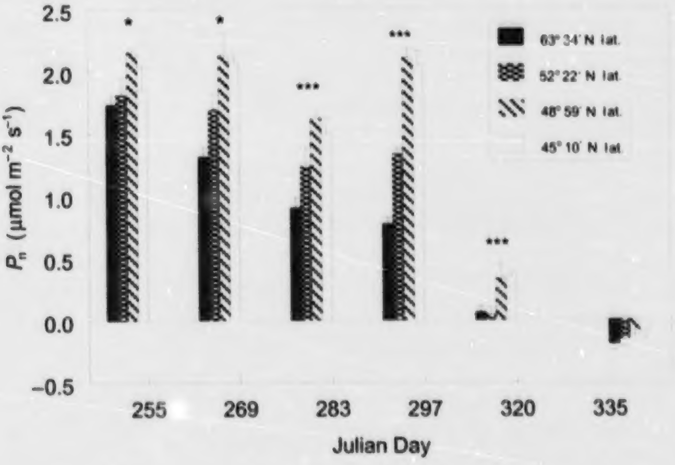
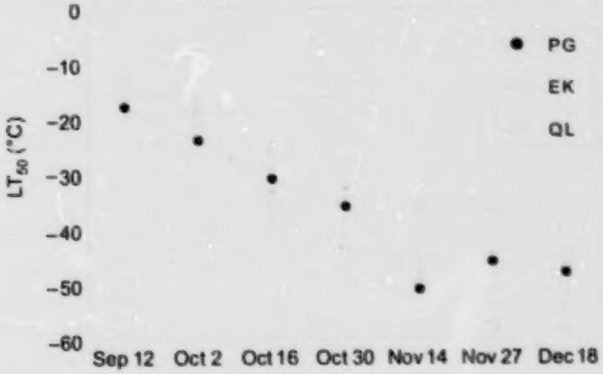


Fig. 4.2*e*. Freezing tolerance (defined by LT$_{50}$, the freezing temperature resulting in 50% needle electrolyte leakage) (mean ± SE) during fall acclimation of interior spruce seedlings from East Kootenay (EK; 50° N lat.), Prince George (PG; 53°22′ N lat.), and Quesnel Lake (QL; 53°13′ N lat.) seedlots (adapted from Binnie et al. 1994).



more northern, compared to southern, latitudes having greater freezing tolerance during fall acclimation (Simpson 1994; Binder and Fielder 1996*b*). Sitka (Cannell and Sheppard 1982; Cannell et al. 1985; McKay 1994) and Norway (Beuker et al. 1998) spruce populations collected from more northern, compared to southern, latitudes also had greater freezing tolerance during fall acclimation.

Identifying phenological, morphological, and physiological differences between populations is very important because these differences in geographic sources can affect their adaptation to local environmental conditions. These differences ultimately affect spruce species growth and survival.

4.3 Genetic variation at the family level

The geographic distribution of plants is influenced, in part, by the ability of plants to respond physiologically in a manner that allows growth to occur under limited water. Spruce species are very sensitive to conditions of low relative humidity (Section 3.2) and limited soil water (Section 3.5.2.1). These limiting environmental conditions can cause a reduction in gas exchange capacity and result in lower growth rates in spruce species. In a series of studies that examined the performance of black spruce families, one female parent (59) produced families that had high productivity on all types of sites, while another female parent (63) produced families that had high productivity on good sites but not on a drought-prone site (Johnsen and Major 1995). These authors conducted a series of studies to describe the physiological mechanisms that influenced productivity of these black spruce families in relation to summer growing season atmospheric and edaphic conditions.

In initial studies, Johnsen and Major (1995) found that the progeny of female 59 had higher P_n than the progeny from female 63 over a number of years of contrasting rainfall and on both wetter and drier sites during a year with summer drought. Johnsen and Major (1995) hypothesized that genetic differences in P_n (i.e., 59 > 63) were maintained under both optimal and limited water conditions and that this genetic variation in P_n would impact on productivity and thus be the mechanism describing the genetic variation in growth rate. When the P_n of progeny from female 59 was compared to that of female 63 across all sites and in summer soil water conditions, the progeny of female 59 had higher a P_n across all Ψ_{pd} conditions (Fig. 4.3*a*). In fact, the P_n values of progeny from female 59 were 12.5 and 7.4% higher than from female 63 on the dry and wet sites, respectively (Major and Johnsen 1996). These findings indicate that progeny from female 59 develop a level of drought tolerance that enables photosynthesis to occur under summertime drought conditions (Section 3.5.2.1).

During the summer growing season, the level of drought tolerance can determine whether or not a species, or genetic source, can withstand drought on a field site (Section 3.5.2.1). Over 3 years of measurement, female 59 progeny had lower Ψ_{sat} than female 63 progeny (Johnsen and Major 1999). In addition, genetic differences in Ψ_{sat} were evident on both dry and wet sites (Fig. 4.3*b*). Stable genetic differences in Ψ_{sat} were maintained between female 59 progeny and female 63 progeny by the same rate of osmotic adjustment from low to moderate water stress that occurred during the growing season (Major and Johnsen 1999). Tree volume growth was related to Ψ_{sat} (Johnsen and Major 1999), leading to the conclusion that Ψ_{sat} was one of the drought tolerance traits that strongly influence the growth of black spruce families across sites of varying soil water availability (Major and Johnsen 1999).

Genetic variation, between progenies of the full-sib families, both in greater gas exchange capacity under all soil water conditions and in osmotic adjustment is part of the drought tolerance strategy inherent in spruce species in general

Fig. 4.3*a*. Models of net photosynthesis (P_n) for black spruce families from female 59 and female 63 during the growing season, in response to decreasing predawn shoot water potentials (Ψ_{pd}). Equations from analysis of covariance are as follows: progeny of female 59, $y = 2.479 + 1.785x$; progeny of female 63, $y = 2.335 + 1.785x$; $r^2 = 0.33$ (adapted from Major and Johnsen 1996).

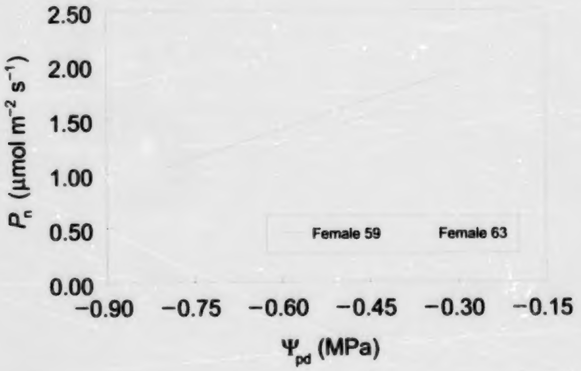
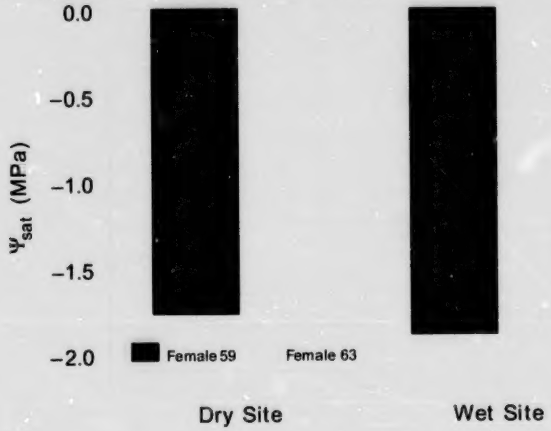


Fig. 4.3*b*. The change in osmotic potential at saturation (Ψ_{sat}) (mean – SE) of black spruce families from female 59 and female 63 during the growing season on wet and dry sites (adapted from Johnsen and Major 1999).

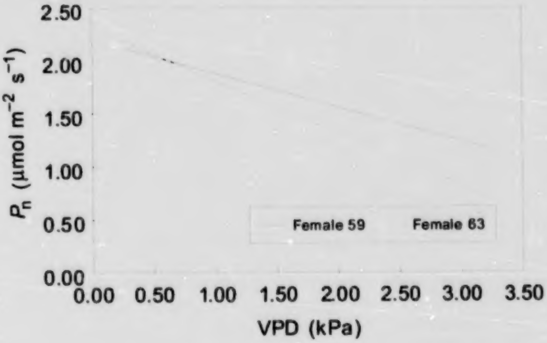


(Section 3.5.2.1). Other work has also shown that fast-growing black spruce families maintained greater P_n and had greater osmotic adjustment under drought conditions, compared with slow-growing families (Tan and Blake 1997). Genetic variation in P_n to declining Ψ has shown both a consistent (Abrams et al. 1990; Kubiske and Abrams 1992; Russell 1993) and shifting (Sands et al. 1984; Bassman and Zwier 1991) pattern between sources as drought stress increased. Other studies have reported no genetic variation to this phenomenon (Parker and Pallardy 1991; Cregg 1994). This drought tolerance strategy has also been identified in Sitka and interior spruce populations that occur with a zone of introgression (Section 4.1), and also at the clonal level for interior spruce (Section 4.4.2).

The daily change in VPD on field sites has a direct influence on the gas exchange capacity of spruces species; P_n decreases with increasing VPD (Section 3.2). Under summer field conditions, as VPD increased, P_n decreased in both black spruce families, although the progeny of female 59 had higher P_n under increasing VPD than the progeny of female 63 (Fig. 4.3*c*). Genetic variation in P_n to changes in VPD also occurs between interior spruce clones (Section 4.4.2).

Long-term WUE of these families found that the progeny of female 59 had higher WUE than the progeny of female 63 (Flanagan and Johnsen 1995). In addition, a consistent difference occurred between measured family $\delta^{13}C$ values over 2 years that had very different precipitation and temperature conditions, which indicated that the family rankings remained fairly constant between years. Flanagan and Johnsen (1995) attributed this greater WUE for progeny of female 59 to improved photosynthetic capacity. The full-sib spruce families used in this trial were a subset of a larger population of out-crossed families where it was found that improved long-term WUE is attributed to greater productivity

Fig. 4.3c. Models of net photosynthesis (P_n) for black spruce families from female 59 and female 63 during the growing season over a range of summertime vapor pressure deficit (VPD) values. Equations from analysis of covariance are as follows: progeny of female 59, $y = 2.203 - 0.322x$; progeny of female 63, $y = 2.309 - 0.497x$; $r^2 = 0.26$ (adapted from Major and Johnsen 1996).



(Johnsen et al. 1999). Researchers have also found that black spruce (Sulzer et al. 1993) and Norway spruce (Larsen and Wellendorf 1990) families with higher instantaneous WUE were generally those that grew better in the field. Work with white spruce has also found that genotypic variation in WUE is attributed to improved photosynthetic capacity and productivity (Sun et al. 1996; Livingston et al. 1999). This suggests that greater WUE in certain spruce genotypes is due to improved productivity in relation to the amount of water that is lost during transpiration.

In this example, black spruce families from one female parent (59) produced families that had a greater physiological capability to respond over a range of soil water conditions or under high evaporative demand conditions that can occur during the growing season. Progeny of this female parent also produced families that display high productivity on all types of sites. The above results on long-term growth data, gas exchange, drought tolerance, and $\delta^{13}C$ data provide evidence that, in this particular case, genetic differences in performance between progeny from female 59 and progeny from female 63 are related to differences in their physiological response on sites of varying soil water availability. This body of work presents a compelling explanation of the physiological mechanisms that define the genetic variation in growth performance between black spruce families from these two differing female parents.

4.4 Genetic variation at the clonal level

Variation exists within populations or stands due to individual tree genotypes. This ability to define the individual uniqueness in performance traits at the clonal level provides advantages in applying clonal forestry to plantation programs. The primary advantages of clonal forestry as defined by Kleinschmit and associates (1993) and Park and associates (1998) are as follows. First is the ability to capture a greater portion of the nonadditive genetic gains from selected individuals within a breeding population. Second is the capability to rapidly introduce individuals with desirable traits to meet known site conditions, specific pest problems, or future products. Third is the ability to carefully plan genetic diversity into plantation programs. Clonal forestry is applied to plantations through clonal propagation. Foresters use various vegetative propagation procedures to incorporate selected clones into plantation forestry programs, and these approaches are discussed later in this treatise (Section 5.1.4.3).

Past work has indicated a large level of genetic variation within spruce species, among families, or individual trees (Khalil 1985). Isoenzyme studies on spruce species (reviewed by El-Kassaby and White 1985) and studies examining morphological development have confirmed this large level of genetic variation (see below). However, little work has been conducted on clonal variation in the ecophysiological performance of spruce species. A number of examples of genetic variation at the clonal level are presented to demonstrate a range of physiological performance and morphological development for a group of interior spruce clones in relation to environmental conditions during selected times of the year.

4.4.1 Morphological variation

Clonal variation in morphological development in spruce species is readily detected at an early age. For example, the morphology of four interior spruce clones after 1 year in the nursery showed variation in development (Table 4.4.1). The clones had a wide range in height and diameter. Measurements of shoot architecture also indicated variation in the number of branches, mean branch length, and branch angle. The clones indicated a wide variation in the potential for growth in the following season; this was based on the wide variation in the number of buds on terminal shoots and needle primordia in terminal buds. The partitioning of dry matter also varied between the clones, indicating clonal variation in biomass allocation patterns. Studies have found large differences in shoot development patterns between families or individual trees of white and interior spruces (Nienstaedt and Teich 1972; Ying and Morgenstern 1979; Kiss and Yeh 1988), and in early shoot and root characteristics between clones of Norway spruce (Kleinschmit and Sauer 1976; Bentzer 1988) and Sitka spruce (Deans et al. 1992). Previous work has found that superior morphological development in the nursery was related to performance in the field (Nienstaedt 1981), while in Norway spruce a 20% selection for height in the nursery gave gains of ~3% in height growth after 6 years in the field (Högberg and Karlsson 1998). However, Kleinschmit and Sauer (1976) warn against intensive clonal selection in Norway spruce early on in a selection program in order to maintain genetic variation for later selection. There is the potential to identify clones with better morphological development in the nursery, although the selection of superior genetic sources cannot be based solely on nursery performance.

For the most part, there was very low variability within any single morphological parameter measured on any single clone. This was due to the genetic

Table 4.4.1. Morphological development ($N = 20$: mean ± SE) of interior spruce clones G351, N366, T703, and W460. Somatic seedlings (i.e., produced from somatic embryogenesis tissue culture) were produced in a containerized nursery culture program as a 1+0 frozen stored stock type in 415B containers.

Measured parameter	G351	N366	T703	W460
Height (cm)	25.8 ± 0.4	22.1 ± 0.5	32.1 ± 1.0	25.2 ± 0.4
Diameter (mm)	3.0 ± 0.1	3.8 ± 0.2	3.9 ± 0.1	3.1 ± 0.1
Number of branches	18.7 ± 0.8	17.2 ± 1.2	13.1 ± 1.3	13.1 ± 1.0
Mean branch length (cm)	3.4 ± 0.1	3.4 ± 0.3	3.1 ± 0.2	2.7 ± 0.1
Branch angle (the degree of upward tilt from perpendicular)	41.3 ± 0.7	44.2 ± 1.0	78.1 ± 2.5	52.4 ± 1.2
Number of buds on terminal shoot	14.4 ± 2.0	14.0 ± 1.1	10.6 ± 0.7	20.2 ± 1.1
Terminal bud needle primordia[a]	159.5 ± 8.4	173.3 ± 12.4	123.6 ± 38.4	132.1 ± 26.9
Needle dry weight (g)	2.0 ± 0.1	1.8 ± 0.1	2.5 ± 0.2	2.2 ± 0.2
Stem dry weight (g)	1.2 ± 0.1	1.4 ± 0.1	1.5 ± 0.1	1.3 ± 0.1
Root dry weight (g)	0.5 ± 0.0	0.8 ± 0.1	1.1 ± 0.1	1.0 ± 0.1
Shoot to root ratio (g/g)	5.5 ± 0.3	4.2 ± 0.4	3.6 ± 0.2	3.6 ± 0.2

Note: Grossnickle and Fan, unreported data.

[a] Needle primordia number was determined on a sample size of eight seedlings.

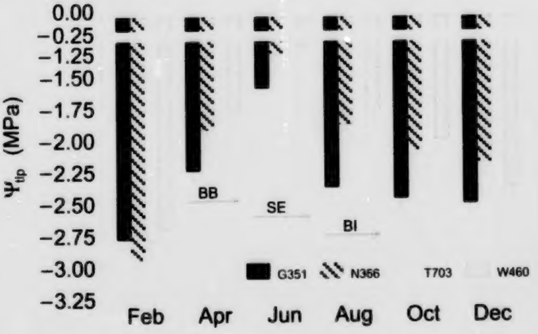
similarity within a single clone (reflected in the low standard errors found in Table 4.4.1). There were large differences in morphological development between these interior spruce clones, and specific clones did not always meet general stock type morphological specifications designed for general spruce containerized seedling populations (Section 5.1.4). This variability in morphological development of clonal spruce stock types is important to recognize when developing stock type morphological standards for clonal material being produced from either a rooted cutting or a somatic embryogenesis tissue culture program.

Variability in morphological development needs to be recognized when seedlings are produced from clonal spruce stock types and improved seed from specific families. Hawkins (1998) recognized that there are a number of potential benefits if seedlings are grown in the nursery in pure rather than bulked mixtures: (*i*) increased seedling quality and crop uniformity, (*ii*) minimized number of culls, (*iii*) enhanced realized gain, (*iv*) ensured genetic composition (i.e., diversity) of the seedling crop, (*v*) no imposed directional selection during nursery production, and (*vi*) family, or clonal, information with respect to nursery cultural practices. On the other hand, if genetic material is viewed as a bulked genetic source, then caution needs to be taken in determining morphological culling standards. This is because the removal of small seedlings could result in directional selection (i.e., removal of certain clones of families) (Campbell and Sorensen 1984). Another concern of intensive grading with the intent of producing uniform planting stock is that this process can possibly eliminate genotypes adapted to harsh and extreme field site environmental conditions (Lang 1989). If uniform stock standards are going to be required for stock produced from selected genetic sources, then these genetic sources may need to be grouped based on morphological development patterns to allow for the application of nursery cultural practices that produce stock with uniform morphological characteristics. Hawkins (1998) cautions that even though there are potential benefits to family, or clonal, segregation when developing seedlings in the nursery, these benefits need to be weighed against the extra costs of increased handling and record keeping.

4.4.2 Physiological variation

The inherent drought tolerance pattern of spruce species changes in a seasonal cycle that is related to phenological state (Section 2.1.1). The Ψ_{tlp} for all clones were at their lowest during the winter months (–2.8 to –3.0 MPa for February) when there was no shoot growth activity (Fig. 4.4.2*a*). There was an increase in Ψ_{tlp} during the spring, when budbreak and shoot growth occurred. During shoot elongation, all clones were at their seasonally lowest level of drought tolerance, and there was a fairly broad range between clones (Ψ_{tlp} of –1.26 MPa for W460 to –1.83 MPa for T703). Genetic variation in osmotic adjustment within a species can occur during the growing season (Bongarten and

Fig. 4.4.2*a*. Changes in osmotic potential at turgor loss point (Ψ_{tlp}) of interior spruce clones ($N = 6$: mean – SE) G351, N366, T703, and W460 throughout the year (Grossnickle and Fan, unreported data). Shoot phenological stages are defined by (BB) budbreak, (SE) shoot elongation, and (BI) bud initiation.



Teskey 1986; Abrams 1988; Collier and Boyer 1989; Tan et al. 1992*b*; Russell 1993; Zine El Abidine et al. 1994*b*). The level of drought tolerance within critical periods of the seasonal cycle, e.g., summer shoot development period, determines whether or not the seedlings can withstand drought conditions on a field site. These differences in drought tolerance may be used to select interior spruce clones that are better suited for planting on reforestation sites prone to summer drought conditions. During the late summer and early fall, after budset occurred, Ψ_{tlp} decreased in all clones, although there were distinct differences in drought tolerance (Ψ_{tlp} of −1.80 MPa for W460 to −2.40 MPa for G351). Clonal differences diminish when clones develop their greatest level of drought tolerance during the winter. Interior spruce clones differ in their ability to adjust water relation parameters in response to seasonal changes, with the greatest variation apparent during the spring and summer shoot development period. These differences can influence drought tolerance, and ultimately, survival and growth potential in the field.

The predictive power of performance assessment, in this case genetic variation, can be increased by developing phenomenological (i.e., descriptive) models under defined environmental conditions (Hall 1982). The dynamic nature of gas exchange of spruce species to light, evaporative demand, and soil water requires a phenomenological modeling approach to capture a representative response pattern to the seasonal range of these environmental variables (Kaufmann 1982*a*; Grossnickle and Reid 1985; Grossnickle and Major 1994*b*). Examples are presented for the gas exchange patterns of four interior spruce clones to changes in light, evaporative demand, and soil water under summer conditions.

During the summer growing season, gas exchange processes of spruce species are primarily influenced by light and evaporative demand when soil water is not limiting (Sections 3.1 and 3.2, respectively). All clones had a rapid increase in P_n up to a PAR of 500 µmol m^{-2} s^{-1}, followed by a gradual increase up to 2000 µmol m^{-2} s^{-1} (Fig. 4.4.2*b*). This same gas exchange pattern is previously described for spruce species (Section 3.1). Genetic variation in P_n to PAR was apparent between the interior spruce clones, with up to a 33% difference in clonal response across higher light (PAR > 500 µmol m^{-2} s^{-1}). Genetic variation in P_n to PAR has been found in a number of tree species (Gordon and Promnitz 1976; Ceulemans and Impens 1980; Bassman and Zwier 1991; Mebrahtu and Hanover 1991; Dunlap et al. 1993). This gas exchange data indicates that interior spruce clones differ in their ability to photosynthesize in response to the daily range of light conditions that occur during the summer growing season.

The VPD at reforestation sites during the summer continually changes in a dynamic fashion and regularly ranges from 0 to 5 kPa (Section 1.3.2). Daily changes in VPD is one of the primary atmospheric variables influencing the gas exchange processes of spruce species when seedlings are under optimum edaphic conditions (Section 3.2). Interior spruce clones showed a decrease in P_n as VPD increased, with genetic variation apparent between the clones (Fig. 4.4.2*c*).

Fig. 4.4.2*b*. The modeled pattern of net photosynthesis (P_n) for interior spruce clones G351, N366, T703, and W460 over a range of summertime photosynthetically active radiation (PAR) (adapted from Grossnickle and Fan 1998). The regression models for each clone are as follows: G351: $y = 1.19 \ln x - 4.52$, $r^2 = 0.46$; N366: $y = 1.17 \ln x - 3.90$, $r^2 = 0.48$; T703: $y = 1.34 \ln x - 5.67$, $r^2 = 0.76$; W460: $y = 1.22 \ln x - 3.76$, $r^2 = 0.47$.

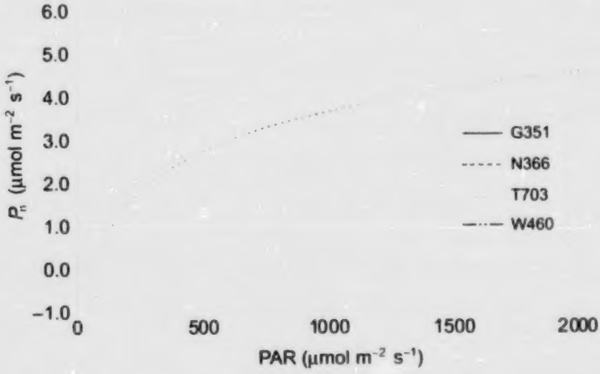
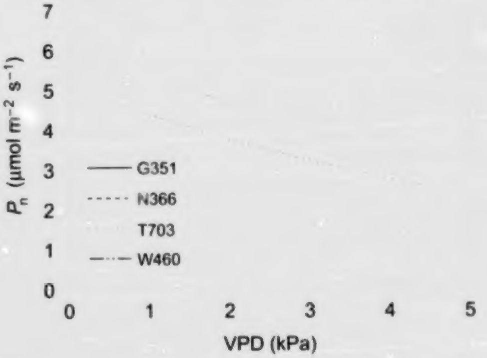


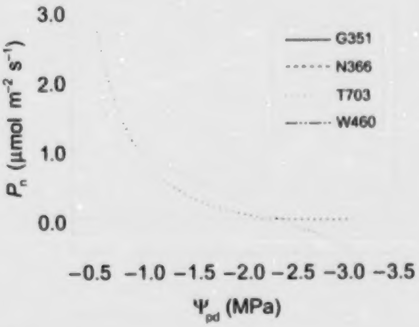
Fig. 4.4.2*c*. The modeled patterns of net photosynthesis (P_n) of interior spruce clones G351, N366, T703, and W460 over a range of summertime vapor pressure deficit (VPD) values (adapted from Grossnickle and Fan 1998). The regression models for each clone are as follows: G351: $y = 5.75e^{-0.17x}$, $r^2 = 0.57$; N366: $y = 5.84e^{-0.11x}$, $r^2 = 0.51$; T703: $y = 5.09e^{-0.16x}$, $r^2 = 0.70$; W460: $y = 6.23e^{-0.15x}$, $r^2 = 0.57$.



As VPD increased from 1.0 to 4.0 kPa, all clones had decreases in P_n with up to a 20% difference in clonal response, although only a slight shift in P_n ranking. Other studies have reported either no shift in P_n ranking (Bassman and Zwier 1991) or different (Bennett and Rook 1978) patterns of P_n decline with increasing VPD between clones of the same tree species.

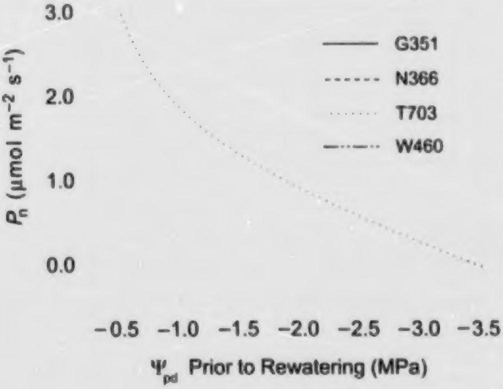
Limited soil water can cause a reduction in gas exchange processes during the summer growing season (Section 3.5.2.1). The drought responses of interior spruce clones revealed only slight genetic variation in P_n to increasing drought (Fig. 4.4.2*d*). Genetic variation in P_n to declining Ψ has been reported for families of spruce and between sources for other tree species (Section 4.3).

Fig. 4.4.2*d*. Models of net photosynthesis (P_n) for interior spruce clones G351, N366, T703, and W460 in response to decreasing predawn shoot water potentials (Ψ_{pd}) (adapted from Fan and Grossnickle 1998). The regression models for each clone are as follows: G351: $y = 0.94 + 0.5x - 0.53/x$, $r^2 = 0.92$; N366: $y = 0.84 + 0.48x - 0.69/x$, $r^2 = 0.87$; T703: $y = 1.52 - 0.27x - 2.08/x$, $r^2 = 0.80$; W460: $y = 0.1 + 0.22x - 0.83/x$, $r^2 = 0.87$.



Recovery of gas exchange capacity from drought stress is dependent upon the level of water stress just prior to watering (Section 3.5.2.1). In this example for interior spruce clones, the recovery of P_n decreased as Ψ_{pd} prior to watering declined from –0.5 to –3.5 MPa (Fig. 4.4.2*e*). Dehydration tolerance of a species can be judged on the basis of physiological recovery from drought stress (Pallardy et al. 1995). Genetic variation in the recovery of P_n, after drought, was found across the whole range of drought conditions, and clonal differences shifted, depending upon the severity of drought stress. Interestingly, clones that exhibited the highest (clone G351) and lowest (clone W460) recovery of P_n after

Fig. 4.4.2*e*. Net photosynthesis (P_n) of interior spruce clones G351, N366, T703, and W460 after rewatering in response to the shoot water potential (Ψ_{pd}) prior to rewatering (adapted from Grossnickle and Fan 1999). The regression models for each clone are as follows: G351: $y = 0.33 - 1.56/x$, $r^2 = 0.92$; N366: $y = 1.28e^{1.3+0.76x}$, $r^2 = 0.68$; T703: $y = 1.35 + 0.49x - 1.0/x$, $r^2 = 0.97$; W460: $y = 0.1 + 0.14x - 1.17/x$, $r^2 = 0.86$.



drought also had the greatest and least, respectively, levels of drought tolerance during the summer growing season (based upon Ψ_{tlp}, Fig. 4.4.2*a*). Recovery of P_n after drought stress is related to the drought tolerance of genetic sources in spruce species (Tan et al. 1992*a*; Fan et al. 1997).

In the fall, spruce species gas exchange processes decline as photoperiods shorten and air temperatures decline (Sections 3.3.1 and 3.9). As temperature and photoperiod declined, P_n decreased in all clones, but the rate of decrease differed between clones (Fig. 4.4.2*f*). Norway spruce also show clonal variation in their P_n to changes in seasonal photoperiods and temperatures (Westin et al. 1995). Thus, it seems that particular genetic sources are better adapted to maintain higher P_n, as overall photosynthetic capacity declines during the fall decrease in temperatures. Maintenance of P_n at low above-freezing temperatures in the fall may be a genetic adaptation of spruce to northern forest climates.

Development of freezing tolerance in northern spruce species normally occurs with seasonal changes in photoperiod and temperature (Section 3.7) during late summer and fall, after shoot growth has ceased. The pattern of freezing tolerance development during the fall differed among the interior spruce clones (Fig. 4.4.2*g*). Genetic variation in freezing tolerance has also been detected in Norway spruce (Westin et al. 1995, 1999) and Sitka spruce (Nicoll et al. 1996) on a clonal basis as well as within full-sib families (Skrøppa 1991). Growing seasons are very short and winters are often very cold in the northern interior of

Fig. 4.4.2*f*. The change in net photosynthesis (P_n) of interior spruce clones ($N = 8$: mean) G351, N366, T703, and W460 with decreasing air and soil temperatures (Grossnickle and Fan, unreported data).

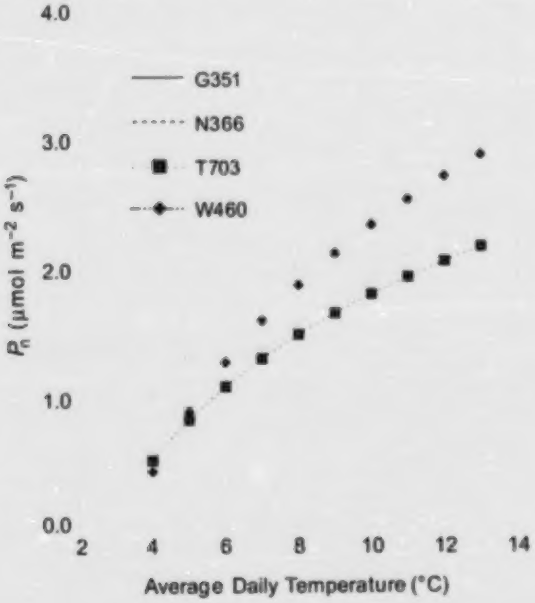
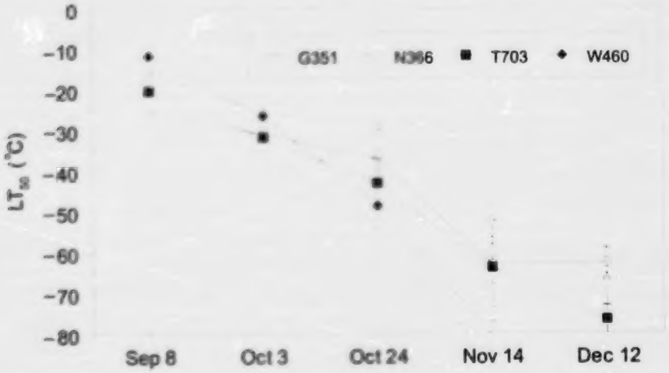


Fig. 4.4.2g. The change in freezing tolerance (defined by LT_{50}, the freezing temperature resulting in 50% needle electrolyte leakage) (mean ± SE) of interior spruce clones G351, N366, T703, and W460 during the fall (adapted from Fan and Grossnickle 1999).



British Columbia (Section 1.2.1). Rapid acquisition of freezing tolerance in the fall would better prepare certain clones to withstand low late-fall and winter temperatures.

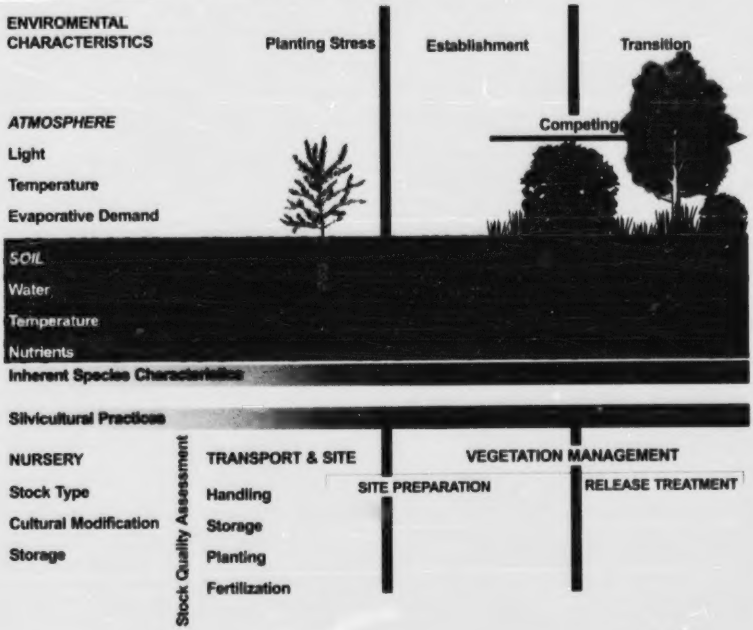
This series of studies provided examples of the clonal variation in interior spruce physiological performance at selected times of the year and within selected environments throughout the yearly cycle. These studies found a wide range in physiological performance between clones in relation to potential field site conditions. Individual clones that had the best physiological performance under drought conditions also had the greatest level of drought tolerance during the summer growing season. Furthermore, certain clones had better photosynthetic response under the full range of both light and VPD. In addition, clonal differences were apparent in the rates of acclimation to fall environmental conditions. This indicates that clonal variation is evident within interior spruce based upon morphological development in the nursery and physiological performance under a range of environmental conditions that typically occur on reforestation sites.

5 Seedling response to silvicultural practices

This section examines the influence of silvicultural practices on the physiological response and morphological development of spruce seedlings during the latter stages of development in the nursery and through early performance on reforestation sites. The forest regeneration process is complex because successful regeneration requires combining an understanding of physiological performance and morphological development characteristics of spruce species with proper silvicultural practices (Fig. 5). Ultimately, seedling performance on a reforestation site depends on the inherent growth potential of the seedling and the degree to which field site environmental conditions limit or enhance this potential.

Nursery cultural and preplanting silvicultural practices have a strong influence on spruce seedling performance immediately after planting. The effects of these practices on seedling performance need to be understood to make sound forest regeneration decisions (Fig. 5). Implicit within this preplanting program is the recognition of the inherent species characteristics when making the selection of the genetic seed source used for seedling production. Proper seed source selection ensures that seedlings are ecophysiologically suited to field site environmental conditions throughout the entire forest rotation (Section 4). Stock quality programs are an effective way of describing the performance potential of seedlings produced from various nursery cultural practices and determining the

Fig. 5. A depiction of the forest regeneration process for spruce seedlings in response to site characteristics and silvicultural practices.


ENVIROMENTAL CHARACTERISTICS
Planting Stress
Establishment
Transition
ATMOSPHERE
Light
Temperature
Evaporative Demand
Competing
SOIL
Water
Temperature
Nutrients
Inherent Species Characteristics
Silvicultural Practices
NURSERY
Stock Type
Cultural Modification
Storage
Stock Quality Assessment
TRANSPORT & SITE
Handling
Storage
Planting
Fertilization
VEGETATION MANAGEMENT
SITE PREPARATION
RELEASE TREATMENT

effects of preplanting silvicultural practices. The discussion starts at the point when final nursery cultural practices are applied to spruce seedlings and thus their implications on seedling field performance. Container-grown spruce seedlings are discussed in subsections on nursery culture effects, stock quality assessment, and stock type development in relation to seedling performance potential. Throughout the remainder of the discussion, information on both container-grown and bare-root spruce seedlings are utilized to examine the effects of preplanting and field site silvicultural practices. The discussion then continues through a logical sequence of operational events by examining storage and handling practices.

The reforestation site is a unique ecosystem, as a forested stand subjected to a disturbance such as harvesting alters the basic structure and function. The altered stand structure influences many processes of the future ecosystem and the microsite environment in which seedlings are to be planted (Section 1). This discussion examines the dynamics of the forest regeneration process within both clear-cutting and partial forest canopy retention silvicultural systems. The intent is to try and define factors that can enhance as well as limit the development of spruce seedlings on reforestation sites.

Newly planted spruce seedlings undergo a series of developmental phases (planting stress, establishment, and transition) on reforestation sites. The length of each phase is dependent upon the response of seedlings to site environmental conditions (Fig. 5). These phases may overlap, depending upon the development of seedlings and competing vegetation. These developmental phases are used to identify and examine each of the processes that can occur after spruce seedlings are planted on a reforestation site. Within each of these plantation development phases, spruce seedling performance is examined in relation to possible site limiting environmental conditions and silvicultural practices (e.g., site preparation, fertilization, and vegetation management) that can possibly mitigate these environmental constraints and improve seedling performance.

Spruce seedling physiological response during these plantation developmental phases determines survival and subsequent growth on reforestation sites. In addition, successful seedling development is affected by not only the past and future silvicultural practices, but also by current and future site environmental conditions (Fig. 5). These conditions continually change due to the development of competing vegetation. Further, vegetation management practices also contribute to plantation development in relation to competition from early successional species. Field performance of spruce seedlings is discussed in context with the interaction between competing vegetation and spruce seedlings during stand development on reforestation sites.

5.1 Nursery and preplanting silvicultural practices

5.1.1 Nursery culture

Nonhardened spruce seedlings lack the physiological capability to tolerate environmental stresses related to drought and freezing temperatures that occur after planting on reforestation sites (Christersson 1972). As a result, nurseries producing containerized seedlings manipulate nursery cultural practices such as day length, water stress, and fertilization regimes to "harden" conifer species (Tinus and McDonald 1979). These practices are intended to improve the capability of seedlings to overcome planting stress and become established on reforestation sites. Each of these cultural practices is briefly reviewed from a historical perspective. The importance of container growing media on seedling performance during establishment is also discussed. In addition, alternative nursery cultural practices designed to improve the drought avoidance capability of conifer seedlings are discussed. Readers are referred to Landis et al. (1989, 1990, 1992, 1999) and Glerum (1990) for further information on nursery cultural practices for producing container-grown conifer seedlings.

5.1.1.1 Short-day treatment

Short-day treatment is a method used on rapidly growing spruce seedlings to induce shoot growth cessation and develop stock with a desired height and diameter. The standard short-day treatment used in operational nurseries is an 8–10-h day and a 14–16-h night for less than 2 weeks (Krasowski et al. 1993*b*). Recent work indicates that the application of only an 8-day short-day treatment (at 16-h night) produced white spruce seedlings with the same morphological and physiological characteristics during the fall hardening process (Coursolle et al. 1998), in addition to dehardening and second-year growth patterns during the spring (Coursolle et al. 1997), as either a 12- or 16-day short-day treatment. The short-day treatment is a widely used cultural practice for containerized white and Engelmann (Arnott and Mitchell 1982; Arnott and Macey 1985), white (Bigras and D'Aoust 1992, 1993; Calmé et al. 1993), black (D'Aoust and Hubac 1986; Colombo et al. 1989; Bigras and D'Aoust 1992), Norway (Christersson 1978), and Sitka (Hawkins et al. 1996) spruce seedlings that are to be fall-lifted for over-winter storage and then planted in the spring. (Seedlings treated with this practice are referred to as short-day spring-planted seedlings.)

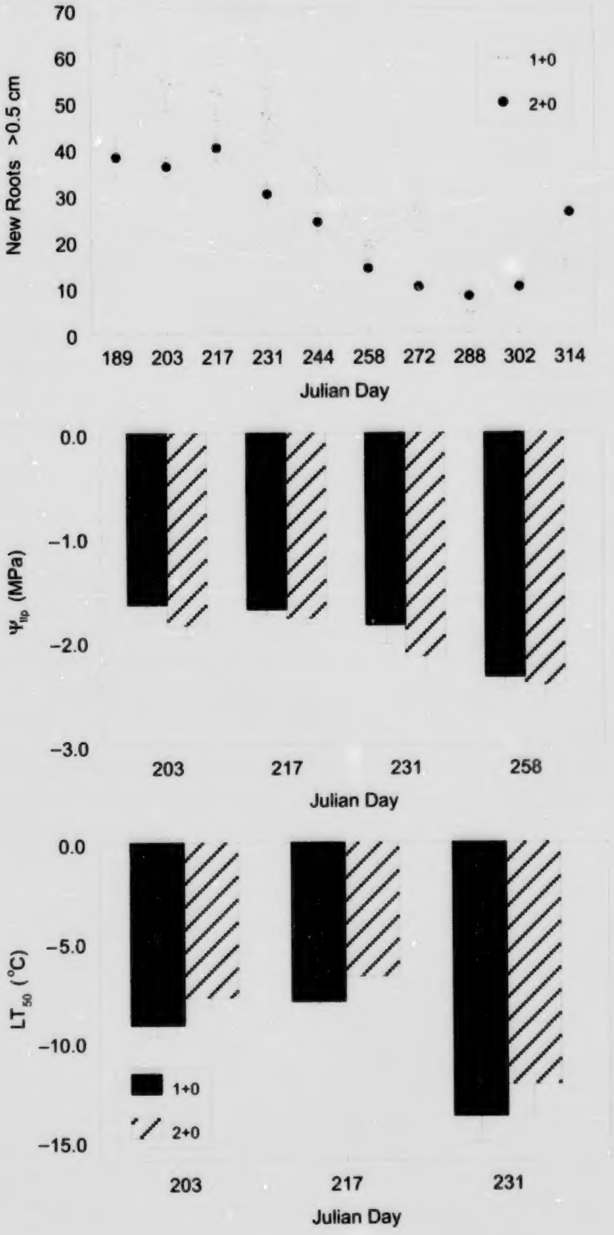
The purpose of this practice is to stop shoot height growth by triggering budset and to promote the development of dormancy, freezing tolerance, and drought tolerance in spruce seedlings during the late summer and fall (Sections 2.5 and 3.9). Interestingly, short-day treatments are also reported to promote P_n while reducing respiration, which provides the needed photosynthates for accelerated root development (Hawkins et al. 1994). Short-day spring-planted seedlings require an adequate time period in the fall for sufficient development of dormancy before being lifted and stored for spring planting (Simpson 1990) (Section 5.1.3). The field performance of spruce seedlings treated with the short-day nursery cultural practice and planted in the spring planting program is discussed in Section 5.4.1.2.

Short-day nursery cultural practices are also used for development of spruce seedlings slated for summer planting. (These seedlings are referred to as short-day summer-planted seedlings.) This practice entails the application of a short-day treatment, usually during June, 3–4 weeks before seedlings are shipped to the field for July or early August planting. The short-day treatment causes seedlings to cease shoot elongation and set a terminal bud prior to shipment to the field. These seedlings usually do not reflush after being planted. This nursery cultural practice is applied to both 1+0 and 2+0 spruce stock types and is believed to "harden" seedlings to enable them to withstand summer field site environmental conditions.

The application of short-day nursery cultural practices for summer-planted seedlings is a new nursery practice, and no published information is available on its implications in hardening spruce seedlings. Recent unpublished work has shed some light on its effects on the ecophysiological performance of spruce seedlings. Short-day summer-planted seedlings (both 1+0 and 2+0 stock types) showed high root growth capacity during the July and early August planting periods (Fig. 5.1.1.1). During this period root growth was higher in the 1+0 compared to 2+0 seedlings. Short-day summer-planted seedlings had good root egress (i.e., root development out of the container plug) on field sites after planting during July and August when soil temperatures were warmer (Revel et al. 1990). During September and into October, root growth declined in both stock types, but started to increase in late October and early November. This cycle of root growth is typical for spruce seedlings going through their fall dormancy cycle (Sections 2.6.2.1 and 3.9). Short-day summer-planted seedlings have a comparatively low level of drought and freezing tolerance, which is similar to actively growing spruce seedlings during the July and August planting season (Sections 2.1.1 and 3.7, respectively). Short-day summer-planted seedlings start to develop a greater level of stress resistance later in the summer, with this pattern being typical of spruce seedlings.

A number of conclusions can be drawn on the effects of short-day treatments on spruce seedlings used in summer planting programs. First, short-day treatments cause the cessation of height growth and the development of a terminal bud, with shoot growth usually not occurring until the start of the next growing season. Second, seedlings go to the field with high root growth capacity, and this, coupled with no shoot growth, can improve both the seedling field establishment and drought avoidance capability through improved root to shoot balance. Third, short-day treatments do not confer improved stress resistance, either freezing or drought tolerance, compared to spruce seedlings that are just completing the active growing phase. Short-day treatments do promote vegetative maturity, and this change in their phenological cycle improves the stress resistance of spruce seedlings as the summer progresses (Section 3.9). Application of short-day treatments are an effective cultural treatment for use on seedlings used in the summer planting program. However, these seedlings still have a low level of stress resistance just after planting, and this should be considered when selecting planting locations on reforestation sites.

Fig. 5.1.1.1. Summer and fall changes in root growth ($N = 24$: mean ± SE), drought tolerance (osmotic potential at turgor loss point, Ψ_{tlp}) ($N = 6$: mean – SE), and freezing tolerance (the freezing temperature resulting in 50% needle electrolyte leakage, LT_{50}) ($N = 8$: mean – SE) of 1- and 2-year-old interior spruce stock types intended for a summer planting program after application of a short-day treatment in mid June (day 166) (Grossnickle and Folk, unreported data).



5.1.1.2 Water stress treatment

The application of a series of water stress events is used as a nursery cultural practice to induce shoot growth cessation in rapidly growing conifer seedlings. Similar to short-day treatments, a series of water stress events at the end of the growing season are applied to trigger budset and the development of dormancy, freezing tolerance, and drought tolerance in spruce seedlings. In British Columbia, Styroblock® containers are dried down to approximately 60% of the postirrigation weight (Matthews 1983). This is comparable to a Ψ_{pd} between –0.5 and –1.0 MPa (Cleary et al. 1978) and is enough to cause a reduction in growth activity (Sections 2.1.3 and 3.5.2.1), although not a total suppression of g_{wv} and P_n in spruce seedlings (Section 3.5.2.1).

This practice of periodic moderate water stress is an effective means to induce bud formation in container-grown interior (Macey and Arnott 1986), white (Calmé et al. 1993), and blue (Young and Hanover 1978) spruce seedlings. Soil Ψ as low as –0.5 MPa had no effect on needle initiation in spruce seedlings, although greater drought stress reduced needle primordia development (Section 2.6.1.1). This indicates that mild water stress levels that trigger budset do not have a detrimental effect on the next growing season's predetermined shoot growth of spruce seedlings. However, a water stress nursery cultural treatment can produce spruce seedlings with overall smaller shoot and root development in the nursery (van den Driessche 1991*b*). Water stress treatments improve freezing tolerance in some conifer species (Timmis and Tanaka 1976; Blake et al. 1979; Grossnickle et al. 1991*a*), but this has not been reported in spruce (D'Aoust and Cameron 1982; Calmé et al. 1993).

Exposing spruce seedlings to repeated cycles of water stress can increase seedling performance under drought conditions (van den Driessche 1991*b*, 1991*c*). This improved response to drought may be due to osmotic adjustment and chloroplast drought resistance, which can improve overall drought tolerance (Section 3.5.2.1). Water stress treatments also seem to improve the drought avoidance capacity of spruce seedlings. A water stress nursery cultural treatment can increase (Zwiazek and Blake 1989) or have no effect (van den Driessche 1991*c*) on stomatal sensitivity to drought. The degree of stomatal sensitivity produced from a drought nursery cultural treatment is dependent upon the severity of the drought; greater drought stress causes greater stomatal sensitivity (Fig. 3.5.2.1*d*). In addition, a water stress nursery cultural treatment can improve the root growth capacity of white spruce seedlings measured just prior to planting (van den Driessche 1991*b*).

The use of water stress as a hardening nursery cultural treatment has received limited acceptance for a number of reasons. First, there is difficulty in implementing a defined drought treatment in an even manner across container growing formats within a nursery environment. This variability in treatment application is due to differences in irrigation application and differences in seedling water use because of the range in transpiring needle surfaces between seedlings of different sizes. Second, when standard peat-based growing media dries, it can become hydrophobic, making it difficult to rewet. Thus, this nursery cultural treatment has not been found to be a consistently successful practice for hardening containerized seedlings within an operational nursery environment (Landis et al. 1989).

There has been a wide acceptance of short-day treatments as the nursery cultural practice to cause shoot growth cessation in containerized conifer seedlings, so periodic drought stress is now used more as an additional nursery cultural treatment to improve the hardiness of summer-planted spruce seedlings. However, little information is available to determine the physiological benefits of using drought stress to improve the drought resistance of summer-planted spruce seedlings.

5.1.1.3 Fertilization treatment

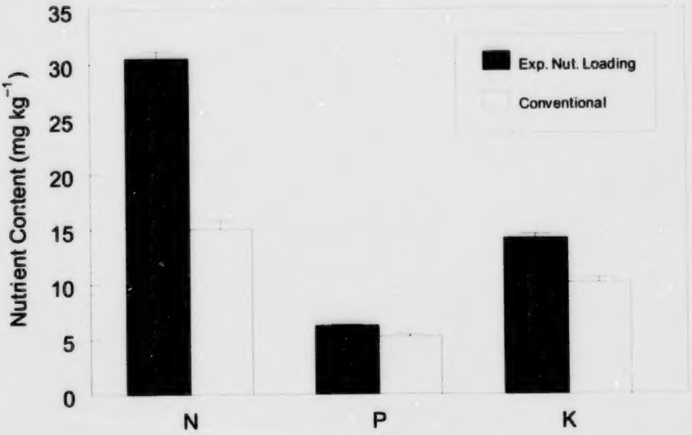
Application of fertilizer in the nursery can be used to both harden containerized spruce seedlings as well as improve their subsequent field performance (Section 5.4.6). The withdrawal of fertilizer towards the end of the growing season is an effective means to slow growth and induce bud formation in container-grown spruce seedlings (Young and Hanover 1978; Macey and Arnott 1986; Bigras et al. 1996). This usually means that the application of N fertilizer is reduced to between 10 and 50% of rates used in the rapid growth phase of seedling development (reviewed by Landis et al. 1989). After spruce seedlings have set buds, the late-summer application of N can either promote (DeHayes et al. 1989; Klein et al. 1989) or have no effect (Calmé et al. 1993) on the development of freezing tolerance during the fall. If the N content in spruce seedlings is too low, the development of freezing tolerance can be delayed, which can limit acclimation during the initial stages of cold hardening in the fall (Bigras et al. 1996). Varying effects of N content on the freezing tolerance of spruce seedlings is dependent upon the interaction of their nutrient content with seedling development throughout the phenological cycle (Section 3.6.2).

Currently, the practice of reducing the fertilizer application is done in concert with the application of short-day treatments during the hardening phase. Miller and Timmer (1997) caution that the use of low fertility hardening regimes can result in the dilution of black spruce seedling nutrient concentrations. This may disrupt steady-state nutrition and adversely affect seedling response after planting. Miller and Timmer (1997) suggest the use of supplemental fertilization during the latter part of the hardening period to increase nutrient levels when seedlings are in a dormant state. This approach is applicable for use with spring-planted seedlings that can continue to receive an adequate supply of all nutrients after they have set bud and during the fall acclimation period in the nursery. However, supplemental fertilization during the latter part of the hardening period may not be appropriate for summer-planted seedlings that are produced in the same year they are planted. As a consequence, spring-planted seedlings may be better suited to sites with low nutrient availability. Recent work has found that spring-planted interior spruce seedlings had a greater ability to buffer the effects of low levels of plant available soil P than summer-planted seedlings due, in part, to a greater internal supply of P and its retranslocation during the growing season (Folk and Grossnickle 2000). Further work is required to address whether the withdrawal of fertilizer during the latter part of the hardening period has a detrimental effect on the performance of summer-planted spruce seedlings on sites with low nutrient availability.

A new fertilization procedure called exponential nutrient loading has been developed to improve seedling performance on competitive reforestation sites (reviewed by Timmer 1997). This nursery fertilization procedure integrates exponentially increasing nutrient additions during the growth phase, with high-dose fertilization towards the end of the growth cycle. This procedure induces steady-state luxury consumption of nutrients through high-dose fertilization to build up nutrient reserves (Fig. 5.1.1.3). The phenomenon of internal nutrient translocation in spruce species is the rationale behind the use of nutrient loading as a nursery cultural practice (Section 3.6.1). Ingestad and Lund (1986) theorized that nutrient loading in the nursery of slow-growing species, such as spruce, would provide seedlings with greater nutrient reserves to utilize after planting on cold northern latitude sites. Thus, nutrient loading may increase the availability of nutrient reserves that are rapidly remobilized to support nutrient demand of new growth once seedlings are planted. Higher nutrient reserves improve the nutrient balance in spruce seedlings and contribute to enhanced stress resistance (Timmer 1997) and increased growth (Section 5.4.6.1).

Ectomycorrhizal fungi normally grow on seedling root systems in the field and are known to enhance growth through the improvement in nutrient uptake

Fig. 5.1.1.3. Nutrient content of spring-planted black spruce seedlings that were treated with either an exponentially increasing fertilization rate (320 mg fertilizer; 64 mg N per seedling) or a conventional constant feed (50 mg fertilizer; 10 mg N per seedling) regime (adapted from Imo and Timmer 1999). Black spruce seedlings in both fertilizer treatments were similar in size (810 ± 73 mg dry mass; $N = 30$) before planting.



and the absorption of soil water (Section 5.4.8). Extensive work has been directed at the inoculation of seedlings with selected mycorrhizal isolates, although normal intensive fertilization practices used to enhance seedling growth in the nursery can limit mycorrhizal development (Castellano and Molina 1989). Exponential fertilization has recently been found to stimulate ectomycorrhizal development on container-grown black spruce seedlings (Quoreshi and Timmer 1998). Quoreshi and Timmer (1998) speculate that higher ectomycorrhizal development in spruce seedlings grown under an exponential fertilization regime is attributed to lower nutrient levels maintained in the growing media. This nursery fertilization approach may provide a way to effectively load spruce seedlings with higher nutrient reserves and increase mycorrhizal development.

5.1.1.4 Growing media

A nursery cultural practice that has received limited attention is the influence of growing-media texture on containerized seedling establishment. In the nursery, coarse (usually peat-based) growing media offer advantages of aeration and low bulk densities for well-watered conditions that are used to stimulate containerized spruce seedling growth (Bernier and Gonzalez 1995). However, after seedlings are planted, soil water contents are rarely optimal.

Under limiting soil water, coarse-textured, compared to fine-textured, growing media cause containerized white spruce seedlings to have lower shoot water potentials (Bernier 1992). This occurs because, as container growing media dries, two things happen. First, coarse-textured growing media, with its large pore spaces, in the container plug loses more water than fine-textured soils with lower soil matric potentials (Day and Skoupy 1971). Second, under low soil water, coarse-textured growing media restrict water flow (low soil hydraulic conductivity, Section 1.3.1) to the part of the seedling root system that is within the container plug (Bernier et al. 1995). As a result, the only parts of the root system of a newly planted containerized seedling that can take up water are the roots on the outer edge of the container plug and those out in the surrounding soil. For example, Engelmann spruce containerized seedling water status was directly related to the balance between the amount of root development out in the soil and the availability of soil water in relation to the needle surface area (Grossnickle and Reid 1984*b*). In this study, roots within the container plug had no effect on the capability of the Engelmann spruce seedling to take up water from the soil. This is one of the causes of increased water stress and subsequent planting stress in newly planted seedlings. Just after planting, the primary active roots absorbing surfaces of a containerized seedling are the roots along the outside of the container plug and the roots that have grown out of the container plug and into the surrounding soil.

It may be worth considering the addition of fine-textured constituents to container media for spruce seedlings to be planted on reforestation sites prone to summer drought conditions. Recent work suggests that adding fine-textured constituents (e.g., sand) to the peat growth media of the container plug improved water retention and soil hydraulic conductivity under low soil water conditions (Heiskanen 1999). As a result, transpiring seedlings in drying fine-textured soils would remain at higher seedling Ψ than seedlings in coarser soils (Bernier 1992). These fine-textured soil additives would allow for greater movement of water from the surrounding soil into the container plug under dry soil conditions, thereby improving the availability of water to seedling root systems.

5.1.1.5 *Alternative nursery cultural practices*

A number of alternative nursery cultural practices have been developed with the intent of improving a seedling's capability to overcome planting stress and to enhance field performance. These cultural practices are designed to improve the drought avoidance capability of seedlings just after planting on the reforestation site. Alternative nursery cultural practices are classified based upon their drought avoidance strategy. One practice minimizes water loss through reduced transpiration, the second increases absorption through the root system, and the third acts to alter the shoot to root balance. Examples of the physiological response of spruce seedlings to each of these types of alternative nursery cultural practices are discussed.

Antitranspirant use is a nursery cultural practice that reduces transpirational water loss through the shoots of conifer seedlings. The concept behind effective use of antitranspirants is that just after planting, the reduction of plant water stress is more important than photosynthesis to ensure growth required for seedling establishment. Antitranspirants reduce transpiration through either a film-type covering of the stomatal pores (Davies and Kozlowski 1974) or through the use of a hormone treatment, such as abscisic acid (ABA), which causes stomatal closure (Davies and Kozlowski 1975).

The use of film-type antitranspirants have shown mixed results when applied to spruce seedlings. Antitranspirants have reduced water loss in black spruce seedlings (Colombo and Odlum 1987). Antitranspirants can reduce the level of water stress (Simpson 1984) or have no effect on seedling water balance (Odlum and Colombo 1987) of newly planted spruce seedlings. Film-type antitranspirants did not reduce the daily and seasonal g_{wv} patterns of newly planted Engelmann spruce seedlings and as a result had no effect on seedling water status throughout the growing season (Grossnickle and Reid 1984*b*). White spruce seedlings treated with certain film-type antitranspirants had less shoot damage and greater survival in a severe drought, compared to control seedlings (Williams et al. 1990). However, certain film-type antitranspirants had negative effects on the root growth capacity and field survival and growth of white spruce seedlings (Simpson 1984).

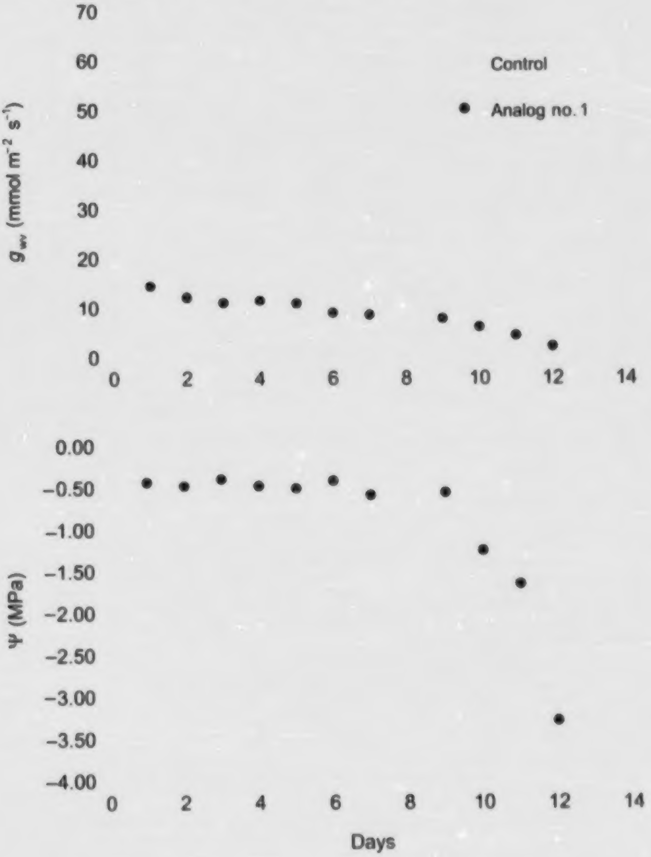
Two general findings can be drawn from these studies. First, film-type antitranspirants have a limited time frame in which they are effective. Over time, the antitranspirant film over the stomatal pore cracks, accounting for the decrease in compound effectiveness (Davies and Kozlowski 1974). Second, there is marked variability in the effectiveness of different antitranspirants in improving the performance of spruce seedlings. Careful selection of antitranspirants is required to ensure their use has a beneficial effect on the performance of spruce species.

As previously discussed, spruce needles have a semipermeable wax plug within the antechamber above each stomatal pore (Section 2.2.1). Jeffree et al. (1971) determined that these wax plugs reduce transpiration to a greater extent than photosynthesis and thus appear to be excellent natural antitranspirants. The anatomical structure of spruce stomata may be responsible for the limited effectiveness of film-type antitranspirants in reducing transpiration rates.

Past studies have found that exogenously applied ABA reduces transpiration in conifer seedlings by closing stomata (Davies and Kozlowski 1975), raising the possibility that ABA could be used as a nursery cultural regime to control water loss in seedlings. Major limitations exist in using ABA within operational forest regeneration programs. The main problems are the following: (*i*) natural ABA is easily degraded and only provides a very short-term effect on stomatal conductance; (*ii*) ABA is poorly absorbed and translocated by some plants; and (*iii*) it is relatively expensive. ABA analogs that are chemically related to natural ABA have the potential to be biologically active in plants, produce similar physiological responses, and are chemically inexpensive to synthesize (Walton 1983; Gusta et al. 1990). Thus, ABA analogs may allow for the development of a cost-effective product to protect seedlings during drought stress. Recent work with ABA analogs has found that specific analogs provide interior spruce seedlings with the capability to maintain good water balance under environmentally stressful conditions through partial stomatal closure (Grossnickle et al. 1996*b*; Fuchs et al. 1999) (Fig. 5.1.1.5*a*). In addition, these ABA analogs have only short-term effects on reducing P_n and g_{wv} (i.e., up to 21 days), thereby maintaining favorable root growth at levels conducive to seedling survival and growth when planted on reforestation sites. This work shows that an ABA analog-based stress avoidance product may help alleviate the initial planting stress in recently planted seedlings.

Root dips are superabsorbent polymers that can absorb hundreds of times their weight in water from the soil. These root dips are designed to increase the soil water that is available to seedlings, presumably by allowing the retained water to become available to seedlings under drought. Root dips are applied by coating the seedling root system with a water – superabsorbent polymer slurry or by mixing the superabsorbent polymer in the planting hole on the field site. The beneficial effects of these root dips on reducing planting stress of seedlings is mixed. When white spruce seedlings were handled carefully, the application of a superabsorbent polymer at the time of planting had no effect on improving Ψ_{min} in response to drought, until severe drought existed (i.e., after day 30) (Fig. 5.1.1.5*b*). There was also little improvement in the water status of white spruce seedlings treated with a superabsorbent polymer under field drought (Magnussen 1986). These findings were confirmed by work showing no beneficial effects of root dips on improved growth and survival of recently planted

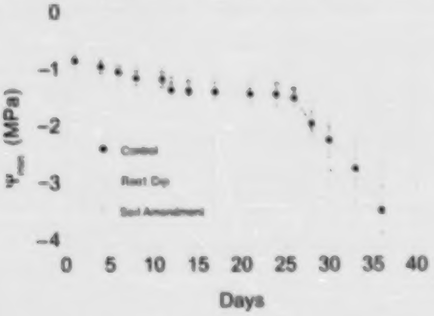
Fig. 5.1.1.5*a*. Needle conductance (g_{wv}) and minimum shoot water potential (Ψ_{min}) (mean ± SE) of container-grown interior spruce seedlings from the control treatment or treated with an ABA analog no. 1 (applied at a concentration of 10^{-3} M) over a severe drought cycle (adapted from Grossnickle et al. 1996*b*).



white spruce seedlings that had been handled properly (Alm 1993; Alm and Stanton 1990). In a review of work done on conifer seedlings, Sloan (1994) concluded that root dips did not improve seedling survival after planting on harsh sites. These root dips are effective in providing protection from desiccation due to improper handling practices (Alm 1993; Alm and Stanton 1990; Sloan 1994), which can reduce the performance of recently planted seedlings (Section 5.1.5).

Nursery cultural treatments are now available that are designed to improve drought avoidance of conifer seedlings through alteration of the shoot to root balance. This cultural treatment is achieved through the application of a plant growth regulator such as paclobutrazol. This growth regulator inhibits the synthesis of gibberellin (Couture 1982), a hormone that promotes shoot growth, reduces dormancy, promotes flowering, and delays senescence in plants (Salisbury and Ross 1992).

Fig. 5.1.1.5*b*. Minimum shoot water potential (Ψ_{min}) of bare root white spruce seedlings ($N = 10$: mean ± SE) from the control treatment or treated with a superabsorbent polymer (Terra-Sorb™), that was applied as a root dip or mixed into the soil, over a severe drought cycle (Grossnickle, unreported data).



The application of paclobutrazol to spruce seedlings has been found to effectively stop shoot growth (van den Driessche 1990; Marshall et al. 1991; Smith et al. 1994). However, the effect of paclobutrazol on root development of spruce seedlings is less clear. Work has found that the application of paclobutrazol can initially reduce root development (van den Driessche 1990; MacDonald 1995) and cause the development of club-like and nodular root thickening (Marshall et al. 1991; Smith et al. 1994). On the other hand, root growth was improved for recently planted white spruce seedlings treated with paclobutrazol (Smith et al. 1994). The application of paclobutrazol also caused stomatal closure in white spruce seedlings, which resulted in a decrease in seedling water stress under drought (van den Driessche 1990; Marshall et al. 1991). Performance of white spruce seedlings treated with paclobutrazol across an entire growing season showed initial water use efficiency improvement with the application of the treatment, although there was no effect during the latter half of the growing season (van den Driessche 1996). Paclobutrazol-treated white spruce seedlings also showed a marked increase in drought resistance by improving turgor maintenance under water stress conditions (Marshall and Dumbroff 1999). Seasonal shoot growth was reduced in white spruce (MacDonald 1995; van den Driessche 1996) and black spruce (MacDonald 1995) seedlings treated with paclobutrazol. Root growth of white spruce seedlings was unaffected when treated with paclobutrazol (van den Driessche 1996), while black spruce seedlings had a dramatic reduction in root growth (MacDonald 1995). van den Driessche (1996) cautions that it would be important in any practical application of paclobutrazol to be able to control the amount taken up by the seedlings because the concentration appears to affect subsequent seedling responses.

In summary, alternative nursery cultural practices have been designed to improve the ability of seedlings to overcome planting stress through improved drought avoidance capability. All of these alternative nursery cultural treatments provide, to some extent, an improvement in the capability of seedlings to withstand stress that can occur just after planting. The benefits derived from these cultural practices depend on proper application of the treatment in the nursery or in the field, and wise selection of reforestation sites where the benefits of these practices improves seedling performance. Foresters need to use discretion when applying any of these alternative nursery cultural practices to seedlings within their forest regeneration program.

5.1.2 Stock quality assessment

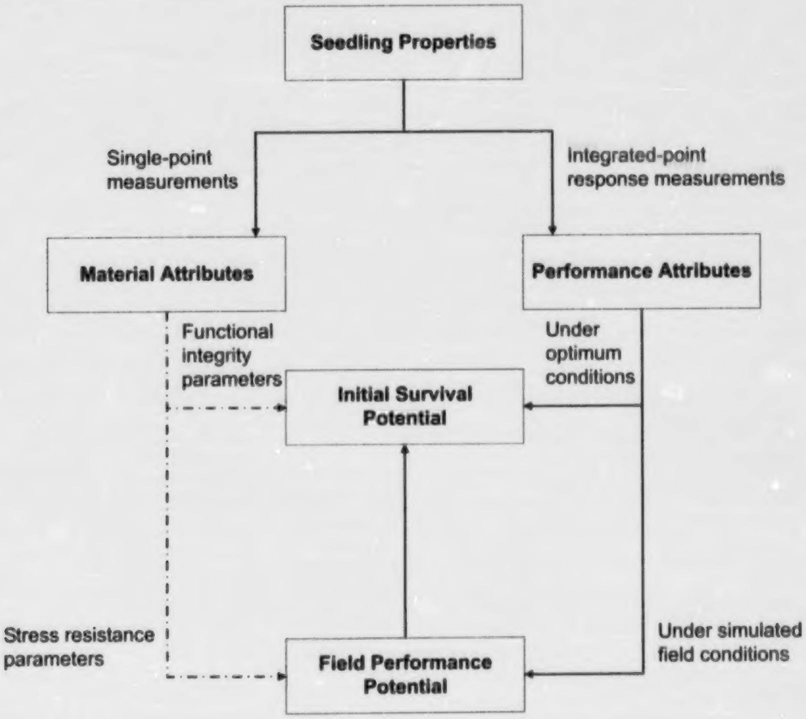
5.1.2.1 General concept

The study of stock quality assessment has evolved over the past 50 years. It is based on the need for a better understanding of performance capabilities for seedlings that are nursery-grown and out-planted on reforestation sites. Wakeley (1954) is usually recognized as the first person to identify the importance of morphological and physiological grading of seedlings prior to planting onto reforestation sites. Stock quality is now defined as the seedling's "fitness for purpose" (Lavender et al. 1980), as it relates to achieving specific silvicultural objectives. Clear and comprehensive stock quality information is necessary to make effective stock selection and field planting choices. In both North America and Europe, stock quality assessment programs are currently used by foresters to ensure quality control, enhance consumer confidence, avoid planting damaged stock, and improve nursery cultural practices (Dunsworth 1997). The following discussion examines both conceptual approaches and testing methods that can be used in conducting a stock quality assessment program.

Stock quality assessment has evolved to include both morphological and physiological tests (see reviews by Sutton 1979; Chavasse 1980; Jaramillo 1980; Schmidt-Vogt 1981; Ritchie 1984; Duryea 1985*a*; Glerum 1988; Lavender 1988; Puttonen 1989*a*; Hawkins and Binder 1990; Johnson and Cline 1991; Omi 1991; Mattsson 1997; Mohammed 1997; Puttonen 1997). The wide array of testing procedures now available has sometimes led to confusion in defining the specific purpose of stock quality assessment. Part of this confusion stems from the fact that stock quality assessment encompasses both nursery development (nursery growth phase, determination of lifting for storage, Section 5.1.3) and testing immediately before planting to determine probable field survival and (or) field performance (Duryea 1985*b*). With a clear definition of purpose for using specific testing techniques, nursery personnel and regeneration silviculturists can focus on obtaining specific information needed to make effective decisions. The following discussion is centered on the importance of assessing quality of planting stock immediately before out-planting to forecast field survival (Section 5.1.2.3) or field performance (Section 5.1.2.4). Due to the widespread use of root growth capacity as a stock quality procedure in reforestation programs, this testing approach is discussed in a separate section (Section 5.1.2.2).

When foresters consider using a stock quality program to assess their seedlings, a commonly expressed concern is how to select tests that are useful for providing information needed to make effective stock selection and field planting choices. A conceptual model has been developed to provide a means of understanding the importance of various testing procedures within a stock quality assessment program (Fig. 5.1.2.1). Determination of stock quality combines measurements of seedling properties that have been defined as material and performance attributes (Ritchie 1984). Material attributes are single-point measures of individual parameters that represent specific seedling subsystems (e.g., morphology, osmotic potential, root electrolyte leakage, nutrient content, individual gas exchange measurements). In contrast, performance attributes reflect an integrated effect of many material attributes, are environmentally sensitive seedling properties, and are measured under specific testing conditions (e.g., root growth capacity, freezing tolerance, 14-day gas exchange integrals). Both attribute types provide information on initial survival potential and field performance potential of seedlings. However, there is no guarantee that testing for initial survival potential provides information on field performance potential under limiting environmental conditions. Foresters need to define the specific silvicultural objectives they hope to achieve with a stock quality assessment program before selection of various testing procedures.

Fig. 5.1.2.1. A conceptual model of the relationship between material attributes, performance attributes, initial survival potential, and field performance potential in stock quality assessment (adapted from Folk and Grossnickle 1997).


Seedling Properties
Single-point measurements
Integrated-point response measurements
Material Attributes
Performance Attributes
Functional integrity parameters
Under optimum conditions
Initial Survival Potential
Stress resistance parameters
Under simulated field conditions
Field Performance Potential

One testing approach that defines the quality of seedlings just prior to planting would be desirable. However, foresters must recognize that no single stock quality test is available for all seedling quality issues (Mattsson 1997; Puttonen 1997). Morphological parameters should not be used to solely assess stock quality, because seedling morphology does not describe the physiological vigor of seedlings (Mexal and Landis 1990). Also, stock quality assessment cannot be determined by individual seedling physiological parameters in isolation from other physiological attributes and morphological characterization (Lavender 1988). Proper stock quality assessment should be done with a combination of morphological and physiological attributes that provide the necessary information needed to make sound seedling-related forest regeneration decisions.

5.1.2.2 Root growth capacity

Seedling root growth is the most common measurement tool used in operational programs throughout the world to define stock quality (Simpson and Ritchie 1997). This assessment approach is determined through a testing procedure called root growth capacity or root growth potential. The importance for a newly planted conifer seedling to grow roots has long been recognized (Wakeley 1954; Stone 1955). Numerous reviews have discussed the merits of measuring root growth within a stock quality assessment approach for determining seedling performance (e.g., Ritchie and Dunlap 1980; Ritchie 1985; Burdett 1987; Ritchie and Tanaka 1990; Sutton 1990).

Root growth capacity is the ability of seedlings to grow new roots under optimum environmental conditions (e.g., 20°C, 18-h photoperiod above a minimum of 25% full sunlight, with optimal soil water and fertility) over a prescribed length of time (e.g., from 7 to 14 days). The test is a quick visual assessment of seedling performance. The universality of root growth capacity in stock quality assessment programs throughout the world indicates the strength of this test to provide foresters with information they need to make seedling deployment decisions. The drawback of this stock quality assessment approach comes in the interpretation of the findings.

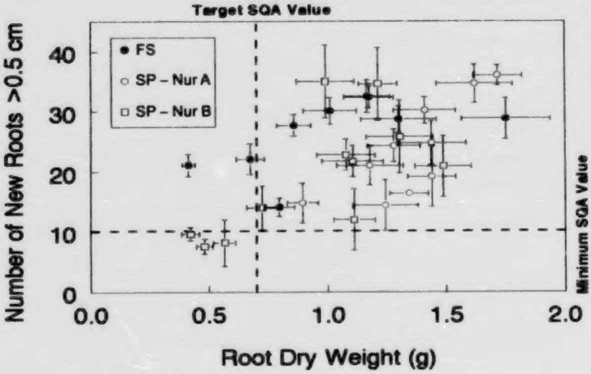
One misconception in interpreting results of root growth capacity testing is that root growth in spruce seedlings is constant over time. As previously discussed, root growth in spruce varies throughout the growing season (Fig. 2.6.2.1*b*). Due to the seasonal periodicity of root growth inherent within spruce species, healthy seedlings sometimes do not grow roots even under ideal environmental conditions (Section 3.9). Seasonal root growth capacity of interior spruce containerized seedlings, for the most part, follow the above-described seasonal pattern (Fig. 5.1.2.2*a*). In frozen-stored seedlings, root growth capacity remains high in storage if the seedlings are lifted and placed in storage when they have a high root growth capacity (Section 5.1.3). Immediately after seedlings are removed from storage, they retain a high root growth capacity which declines as seedlings begin shoot growth. The decline in root growth capacity continues during bud development and through the fall until dormancy intensity weakens. Thereafter,

Fig. 5.1.2.2*a*. Seasonal pattern of root growth capacity (i.e., number of new roots) for container-grown interior spruce seedlings ($N = 24$: mean ± SE). Measurements recorded in December through April (i.e., outside of dashed lines) were taken on seedlings removed from frozen storage (Grossnickle, unreported data).

root growth capacity increases and remains high in storage. If seedling quality is based solely on root growth capacity, at certain times of the year false assumptions can be made that seedlings are of poor quality. It is recommended that a more comprehensive stock quality testing approach be considered, which provides not only an assessment of root growth capacity of seedlings but also an understanding of seedling stress tolerance and physiological response to potential reforestation site environmental conditions (Section 5.1.2.4). In this way, a measure of root growth capacity can then be placed in context with the overall quality of the seedlings.

Another misconception in interpreting results of root growth capacity is that a single numerical scale is applicable for assessing root growth capacity under all operational conditions. Studies have found that root growth capacity changes because of the following parameters: species differences, genetic variation within a species, seedling size, and nursery cultural practice. For example, Engelmann spruce seedlings have lower root growth capacity than lodgepole pine seedlings grown under the same nursery cultural conditions (Ritchie et al. 1985). Root growth capacity has also been reported to vary between populations of black spruce seedlings raised under the same nursery cultural regime (Sutton 1983). This also occurs in interior spruce seedlings growing under the same nursery cultural regime and having a similar root system size (Fig. 5.1.2.2*b*). Root growth capacity of seedlings also changes with the size of the root system; greater new root growth occurs with a greater original root system size. Studies have shown that greater initial root mass is related to greater root growth capacity in pine (Johnsen et al. 1988; Williams et al. 1988) as well as in interior spruce (Grossnickle and Major 1994*b*) seedlings. Root growth capacity of spruce seedlings also varies, depending upon whether the stock type was grown and then stored for a spring planting program or fresh-lifted for a summer planting

Fig. 5.1.2.2*b*. Relationship between root dry weight and the root growth capacity (determined over 14 days; $N = 15–25$: mean ± SE) for 30 clonal populations of container-grown (415-B) interior spruce seedlings. Clonal populations of seedlings came from a series of operational regeneration silvicultural practices: (*i*) spring-planted frozen-stored (FS), (*ii*) fresh-lifted for summer planting and grown at nursery A (SP – Nur A), or (*iii*) fresh-lifted for summer planting and grown at nursery B (SP – Nur B) (Grossnickle, unreported data). Minimum or target stock quality assessment (SQA) values are defined in Table 5.1.4.1.



program (Fig. 5.1.2.2*b*). In addition, the root growth capacity of spruce seedlings varies, depending upon the cultural practices used by each nursery. Foresters must recognize that the capability of a seedling to grow roots can be influenced by many varying factors. As a result, it is difficult to standardize root growth capacity measurements taken under varying operational conditions.

A major problem with the use of root growth capacity for seedling quality assessment is the assumption that this test is an adequate approach for the prediction of survival and (or) growth of seedlings planted on reforestation sites (reviewed by Simpson and Ritchie 1997). There is a variable relationship between root growth capacity and field performance. Whether or not newly planted seedlings initially require new root growth for proper field performance is related to the planting stress phenomenon (Section 5.3). Briefly, planting stress occurs when a newly planted seedling has transpirational demands that exceed the ability of the root system to take up water from the soil system. One way planting stress is relieved is when root growth occurs and seedling water stress is reduced. Simpson and Ritchie (1997) believe that root growth capacity is strongly related to field performance when stock has an inherently low level of stress resistance and when site environmental conditions become more severe. These are conditions that lead to planting stress. However, if seedlings are not exposed to planting stress, then initial root growth is not essential for proper field performance. Simpson and Ritchie (1997) indicate that root growth capacity has no relationship to field performance when seedlings have an inherently high level of stress resistance and when site environmental conditions are mild.

What then does the measure of spruce root growth capacity provide to foresters as a stock quality measurement procedure? First, root growth capacity determines whether seedlings can grow roots within a defined time frame of the phenological cycle. Second, root growth capacity provides an indirect measure of the overall physiological condition of the seedling. If the seedling can grow roots, then all physiological processes that are required for root growth are functional. In other words, the testing approach is a measure of the functional integrity of the seedling, and it is a useful stock quality test that can determine seedling survival potential (Section 5.1.2.3). For example, if information is needed on seedling root growth under various limiting edaphic conditions (e.g., low soil temperature or low soil water, Table 5.1.4.1), root growth capacity testing procedures can be developed to assess performance in relation to these potential reforestation site environmental conditions (Section 5.1.2.4). Root growth capacity testing used in combination with an array of other stock quality testing procedures can provide information on the field performance potential of seedlings (Sections 5.1.2.4 and 5.1.4). Root growth capacity testing can provide foresters with an effective stock quality measurement procedure, but only when it is used with a proper understanding of its strengths and weaknesses.

5.1.2.3 Survival potential testing

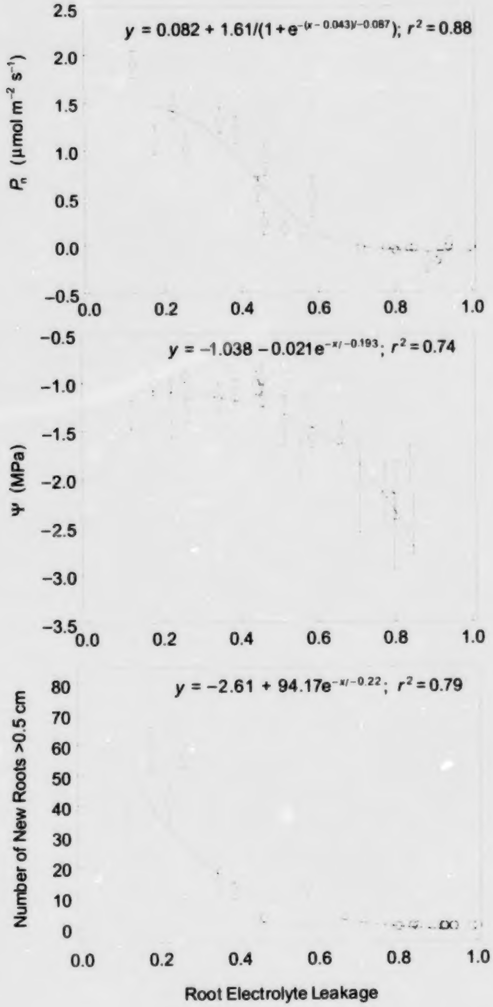
Initial survival potential is a measure of seedling "functional integrity." Functional integrity indicates whether stock is, or is not, damaged to the point of limiting primary physiological processes (Grossnickle and Folk 1993). The intent of these testing procedures are to remove seedlings that do not meet certain minimum physiological performance standards (i.e., the "bad apple concept"). Seedlings that meet minimum standards probably have a greater capability to survive in all but the most severe of field site environmental conditions (Sutton 1988). At present, there are a number of testing procedures that provide information on the initial survival potential of operationally produced stock. A number of these testing approaches are defined in Table 5.1.2.3. These types of tests measure seedling vitality under a specific set of conditions that define a certain level of quality when tested (Ritchie and Tanaka 1990; Langerud 1991). These tests have been developed for the purpose of batch-culling poorly grown and handled seedlings. They are used to categorize large groups of seedlings, all having a similar nursery cultural regime, or all from a similar seed source, by measuring a subsample from the entire population. Further specific information on each testing procedure can be found in the cited articles.

Measurement of seedling functional integrity helps determine the survival capability at the time of planting. An example of a testing program used to measure the initial survival potential of interior spruce is shown in Figs. 5.1.2.3*a* and 5.1.2.3*b*. In this example, spruce root systems were damaged to varying degrees just prior to stock quality testing. One day after exposure to damaging conditions, root systems were assessed for the degree of damage based upon the root electrolyte leakage procedure (greater root electrolyte leakage value means greater cell membrane damage, thus greater root damage). Seedlings were then

Table 5.1.2.3. Examples of stock quality tests that measure the initial survival potential of seedlings immediately before planting.

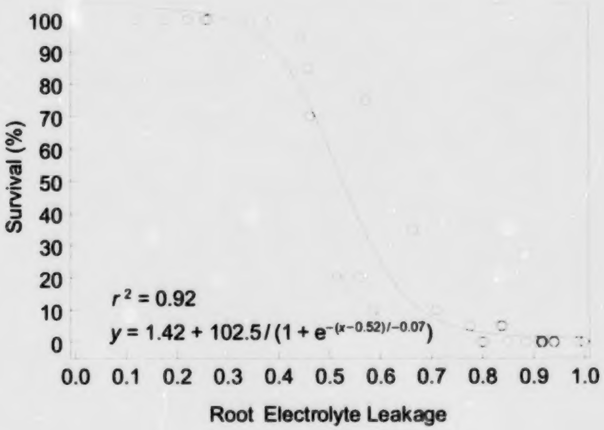
Stock quality tests	Test purpose	References
Root growth capacity (optimum environment)	A measure of seedling ability to regenerate new roots and an indirect measure of seedling physiological condition (Section 5.1.2.2).	Stone 1955; Ritchie and Dunlap 1980; Ritchie 1985; Burdett 1987; Ritchie and Tanaka 1990; Sutton 1990; Simpson and Ritchie 1997
Vigor test	Expose seedlings to a stress event and then measure subsequent seedling survival.	McCreary and Duryea 1985, 1987; Lavender 1988
Shoot water potential	Measurement of Ψ as an indirect measure of root system capability to absorb water.	McCreary and Duryea 1987; McKay and White 1997
Needle conductance, transpiration, or photosynthesis	Measurement of gas exchange as an indirect measure of root system capability to absorb water.	Örlander and Rosvall-Ahnebrink 1987; Langerud et al. 1991
Infrared thermography	Measurement of needle temperature as an indirect measure of gas exchange and the root system capability to absorb water.	Weatherspoon and Laacke 1985; Örlander et al. 1989
Root system water loss capability	Measurement of root system water loss under positive pressure as an indirect measure of root system integrity.	Ritchie 1990
Fine root electrolyte leakage	Measurement of root electrolytes as an indirect measure of root system integrity.	McKay and Mason 1991; McKay 1992; Bigras and Calmé 1994; Bigras 1997; McKay and White 1997; McKay 1998
Enzymatic activity	Determination of whether cell tissue is damaged or dead.	Lindström and Nyström 1987; Puttonen 1989*b*
Chlorophyll fluorescence	Direct measure of photosynthetic capacity and an indirect measure of seedling overall quality.	Vidaver et al. 1989, 1991; Binder et al. 1997
Stress-induced volatile emissions	A measure of anaerobic respiration due to cell injury.	Hawkins and DeYoe 1992; Templeton and Colombo 1995

Fig. 5.1.2.3*a*. Stock quality assessment procedures to determine the initial survival potential of interior spruce seedlings with damaged root systems. Damage to the root system of seedlings ($N = 8$: mean ± SE) was determined by root electrolyte leakage (1 day after stress), net photosynthesis (P_n), shoot water potential (Ψ) (1 week after stress), and root growth capacity (2 weeks after stress) (Grossnickle and Folk, unreported data). Seedlings were grown under optimum environmental conditions during the entire assessment period.



grown under optimum environmental conditions and assessed at 1, 2, and 8 weeks by P_n and Ψ, root growth capacity, and survival testing approaches, respectively. Greater root damage resulted in seedlings having lower P_n and Ψ at 1 week, indicating that damaged root systems could not take up water, thus seedlings were under stress and P_n declined. Greater root damage also resulted in

Fig. 5.1.2.3*b*. Stock quality assessment of interior spruce seedlings with damaged root systems measured by root electrolyte leakage (1 day after stress) (subpopulation of $N = 8$) and survival ($N = 25$) (8 weeks after stress) (Grossnickle and Folk, unreported data). Seedlings were grown under optimum environmental conditions during the entire assessment period.



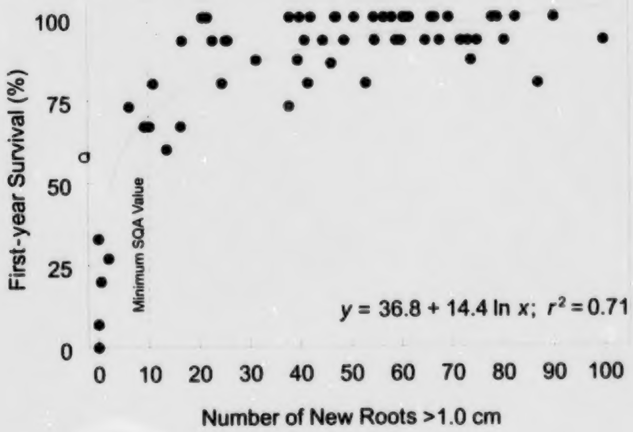
lower root growth capacity after a 2-week test. In addition, interior spruce seedlings with greater degrees of root damage had greater mortality (Fig. 5.1.2.3*b*). Thus, lower functional integrity can also indicate reduced survival potential.

This example demonstrates that stock quality assessment tests are capable of measuring the functional integrity of interior spruce seedling root systems suspected of being exposed to damaging conditions. Very rapid testing procedures, such as root electrolyte leakage, chlorophyll fluorescence, and stress-induced volatile emissions, have the ability to forecast seedling performance for up to 8 weeks after exposure to a damaging event. If there is suspected damage to the shoot system, material attributes that measure gas exchange or photochemical processes are best suited to quickly detect the functional integrity of the shoot system (Table 5.1.2.3). Further testing of performance attributes (e.g., root growth capacity) is required if material attribute testing detects shoot damage.

Seedlings that have reduced functional integrity can have poor field survival. As shown in Figs. 5.1.2.3*a* and 5.1.2.3*b*, spruce seedlings that cannot grow roots have a low survival capability. This same phenomenon can occur in spruce seedlings that are planted on reforestation sites; low root growth capacity results in low field survival (Fig. 5.1.2.3*c*). In fact, this trend was still evident for the survival of interior spruce seedlings after 5 years (Simpson and Vyse 1995).

Measuring root growth capacity can predict field survival when seedlings have low to average stress resistance and when seedlings are planted on sites with limiting environmental conditions (Simpson and Ritchie 1997). This rationale has led to the conclusion that both bare-root (Burdett and Simpson 1984) and container-grown (Simpson et al. 1988) spruce seedlings have a natural root

Fig. 5.1.2.3c. The relationship between first-year survival on a reforestation site and the capability of interior spruce seedlings to grow roots at the time of planting. Each point represents mean survival and mean root growth capacity of five seedlings taken from the same sample population (adapted from Simpson 1990).



growth capacity threshold of an average of 10 new roots (>1.0 cm in length) per plant, which is used as a batch culling guideline in British Columbia. Spruce seedlings with low root growth capacity (<10 new roots) have the potential for poor survival, which results in a greater chance of plantation failure. This guideline has provided a means for defining the risk of planting seedlings on reforestation sites that do not meet this minimum root growth capacity standard. The capability of a spruce seedling to grow roots can be influenced by many varying factors (Section 5.1.2.2). Thus, caution should be used in assuming that a standardized root growth capacity guideline, taken under varying operational conditions, is always representative of the functional integrity of the seedlings.

5.1.2.4 Performance potential testing

Seedling performance on a reforestation site depends on inherent growth potential of the seedling and the degree to which field site environmental conditions limit or enhance this potential. Thus, the degree to which seedlings are suited to site conditions has the greatest influence on seedling performance immediately after planting (Burdett 1983). Seedling characteristics that accurately determine field growth are needed to define the intrinsic performance potential of planting stock to site conditions (Sutton 1982, 1988). As a result, seedling performance potential should be characterized in relation to anticipated field site environmental conditions (Duryea 1985*b*; Sutton 1988; Puttonen 1989*a*; Grossnickle et al. 1988, 1991*a*, 1991*b*; Hawkins and Binder 1990) (Fig. 5.1.2.1). In addition, an array of morphological and physiological tests that examine factors important for determining seedling field performance potential is required because stock quality reflects the expression of a multitude of physiological and morphological attributes (Ritchie 1984; Grossnickle et al. 1991*a*, 1991*b*). A program that measures seedling response to simulated primary planting site environmental conditions can provide information on field performance potential (Grossnickle et al. 1991*a*, 1991*b*; Folk and Grossnickle 1997). Thus, field performance potential testing is a measure of seedling physiological stress resistance capability. This testing approach describes how seedlings physiologically respond to potential reforestation site environmental conditions.

Based on stress tolerance and avoidance concepts defined by Levitt (1980), performance potential tests have been developed to measure seedlings physiological response and morphological development under a range of environmental conditions. Examples of tests that can be used to assess field performance potential are shown in Table 5.1.2.4. Seedlings are normally exposed to some type of stress after planting on a reforestation site (Sections 5.3 and 5.4). As a result, stock quality tests conducted in a defined stress environment have a higher capability to forecast field performance potential. In developing test environments, predominant environmental conditions that seedlings are normally exposed to in the field need to be defined. Test environments should be developed to match the range and combination of anticipated environmental conditions seedlings can be exposed to just after planting on the reforestation site. The anticipated environmental conditions can be defined by silviculturists during onsite development of regeneration prescriptions.

It is necessary to test a combination of attributes in order to develop a comprehensive picture of seedling performance potential. Field performance potential is determined by material attributes that measure or define stress tolerance, avoidance, or resistance and by performance attributes under simulated site environmental conditions (Grossnickle et al. 1991*a*, 1991*b*; Folk and Grossnickle 1997). Figure 5.1.2.4*a* provides examples of field performance potential testing programs that can be applied to seedlings slated to be planted on field sites with anticipated cold or drought environmental conditions. Attribute selection varies, depending upon both the anticipated field site environmental conditions and the defined needs of the end-user. Testing for field performance potential is designed to allow the user to obtain information on stock to meet a defined purpose. This testing program usually falls into one of two categories.

First, field performance potential assessment can be measured on healthy seedlings to define field performance potential in relation to optimum, as well as possible, limiting field site conditions. An example of this stock quality assessment procedure is presented in Section 5.1.4 to describe interior spruce containerized stock types used in spring and summer planting programs and for container-grown seedlings of various sizes.

Second, field performance potential assessment can be determined on seedlings with minor damage where performance and survival is limited under stressful conditions, but not under optimal environmental conditions. An example of this stock quality assessment procedure follows.

Measuring field performance potential of seedlings with minor damage helps determine whether field performance is limited at the time of planting. An example

Table 5.1.2.4. Examples of material and performance attributes used for stock quality testing and their intended purpose for defining field performance potential.

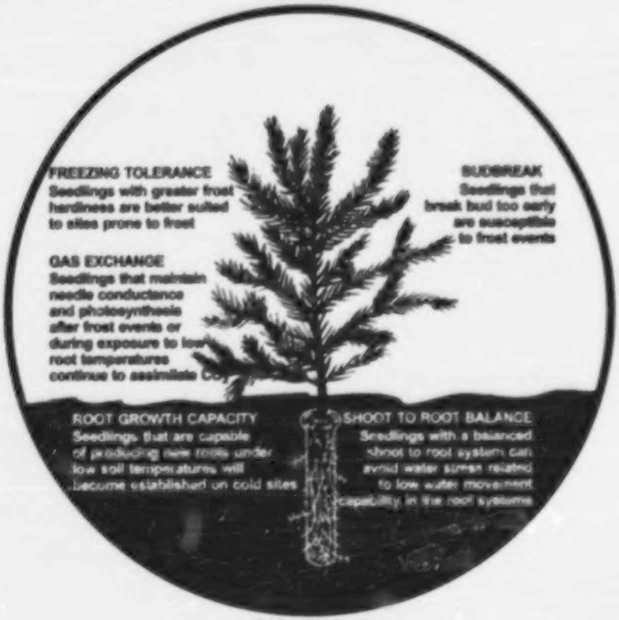
Attribute	Test purpose	References
Material attributes		
Height	General measure of P_n capacity and transpirational area; advantage on sites with brush competition; reflection of potential height growth.	Armson and Sadreika 1979; Cleary et al. 1978; Mexal and Landis 1990
Diameter	General measure of seedling durability, root system size, and protection from drought and heat damage.	Cleary et al. 1978; Mexal and Landis 1990
Height to diameter ratio	General measure of shoot sturdiness.	Mexal and Landis 1990
Root dry weight	Indicator of root absorptive surface.	Thompson 1985
Shoot to root ratio	Measure of seedling drought avoidance potential.	Thompson 1985
Bud length, bud volume, needle primordia	General measure of predetermined shoot extension.	Kozlowski et al. 1973; Colombo 1986
Number of branches and buds	Indicator of seedling growth potential.	Grossnickle et al. 1991*a*
Osmotic potential at turgor loss point (Ψ_{tlp})	Quantitative measure of drought tolerance.	Tyree and Jarvis 1982
Cuticular transpiration	Ability of needles to avoid water loss after stomata have closed.	Vanhinsberg and Colombo 1990
Mineral nutrient status	Indicator of general seedling health and growth potential.	Ingestad 1979; Timmer 1997; Section 5.4.6.1
Carbohydrate reserves	Indicator of general seedling health and growth potential.	Marshall 1985
Days to terminal budbreak	Measure of bud dormancy and indirect measure of changes in drought and freezing tolerance.	Lavender 1985; Burr 1990

Table 5.1.2.4 (*concluded*).

Attribute	Test purpose	References
Performance attributes		
Root growth capacity	General indicator that all systems in a seedling are functioning properly and a measure of seedling performance potential (Section 5.1.2.2).	Ritchie 1984; Burdett 1987
Root growth capacity at low root temperature or after drought	Measure of seedling performance potential under limiting edaphic conditions.	Ritchie 1985; Grossnickle et al. 1991*a*
Freezing tolerance	Measure of seedling tolerance to freezing temperatures.	Glerum 1985
P_n over optimum conditions (14-day)	Measure of seedling photosynthetic capacity.	Grossnickle et al. 1991*a*
P_n over low root temperature conditions (14-day)	Measure of seedling tolerance to cold soils.	Grossnickle et al. 1991*a*
P_n after drought	Measure of seedling drought tolerance in response to a defined level of water stress.	Grossnickle et al. 1991*a*

of a testing program to measure the initial field performance potential of spruce is shown in Fig. 5.1.2.4*b*. These container-grown interior spruce seedlings, destined for a summer planting program, were originally grown under optimum conditions in a greenhouse during early spring. The seedlings were then moved into an outdoor compound where they were inadvertently exposed to stressful atmospheric conditions (i.e., high VPD and light) during the late spring. Although the seedlings were kept well watered, the needles developed sun-scald, or a bleaching of the upper surface of the needles. Seedlings from across the full range of sun-scald conditions were capable of growing roots (all seedlings grew >80 new roots) under the optimum environmental conditions of a standard root growth capacity test. Seedlings were also tested to determine whether the needle sun-scald would affect drought avoidance capability. Both a material attribute test (cuticular transpiration) and a performance attribute test (change in Ψ under drought) indicated that sun-scalded seedlings lacked adequate drought avoidance capability. These sun-scalded interior spruce seedlings had damaged needles that would have limited their performance and survival under drought on a reforestation site. This type of information on seedling quality could only have been determined with the use of performance testing designed to assess drought avoidance capability.

Fig. 5.1.2.4*a*. Possible stock quality testing procedures for determining spruce seedling field performance potential in response to either cold or drought reforestation site environmental conditions.



FREEZING TOLERANCE
Seedlings with greater frost hardiness are better suited to sites prone to frost

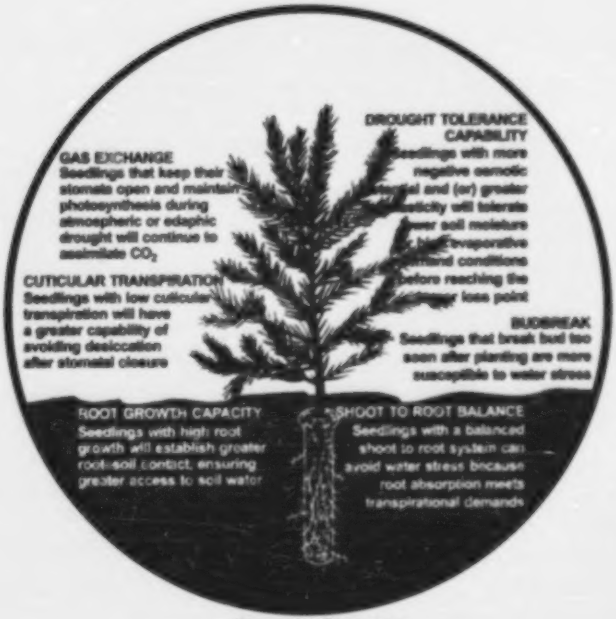
GAS EXCHANGE
Seedlings that maintain needle conductance and photosynthesis after frost events or during exposure to low root temperatures continue to assimilate CO_2

BUDBREAK
Seedlings that break bud too early are susceptible to frost events

ROOT GROWTH CAPACITY
Seedlings that are capable of producing new roots under low soil temperatures will become established on cold sites

SHOOT TO ROOT BALANCE
Seedlings with a balanced shoot to root system can avoid water stress related to low water movement capability in the root systems

Cold Stresses



GAS EXCHANGE
Seedlings that keep their stomata open and maintain photosynthesis during atmospheric or edaphic drought will continue to assimilate CO_2

CUTICULAR TRANSPIRATION
Seedlings with low cuticular transpiration will have a greater capability of avoiding desiccation after stomatal closure

DROUGHT TOLERANCE CAPABILITY
Seedlings with more negative osmotic potential and (or) greater elasticity will tolerate lower soil moisture or high evaporative demand conditions before reaching the turgor loss point

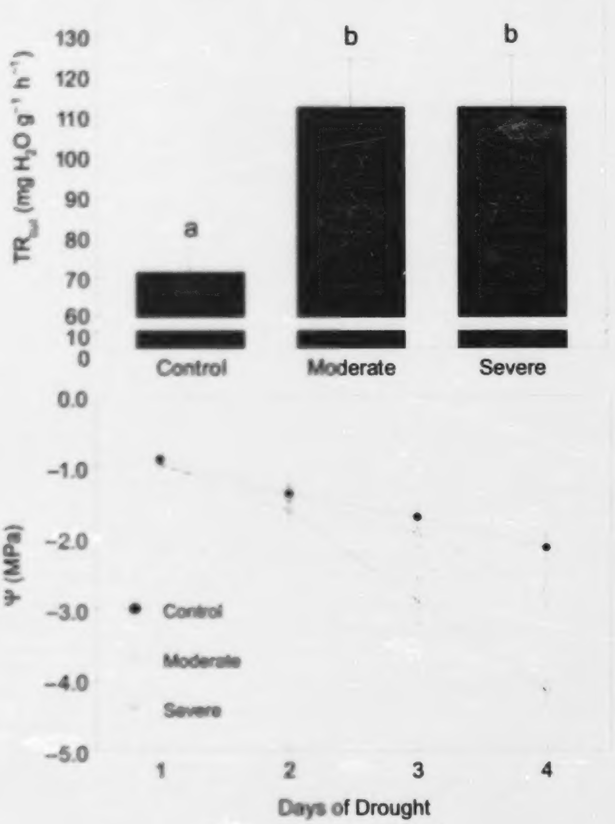
BUDBREAK
Seedlings that break bud too soon after planting are more susceptible to water stress

ROOT GROWTH CAPACITY
Seedlings with high root growth will establish greater root-soil contact, ensuring greater access to soil water

SHOOT TO ROOT BALANCE
Seedlings with a balanced shoot to root system can avoid water stress because root absorption meets transpirational demands

Drought Stresses

Fig. 5.1.2.4b. Stock quality assessment of interior spruce seedlings with varying degrees of needle sun-scald (i.e., moderate and severe) measured by performance potential testing under drought (material attribute: cuticular transpiration (TR_{cut}) ($N = 6$: mean + SE); performance attribute: change in shoot water potential (Ψ) under drought ($N = 8$: mean ± SE)). Letters on the bar graph represent whether seedlings from different damage categories were significantly different as determined by an ANOVA and Tukey's mean separation test ($p = 0.05$) (Grossnickle and Folk, unreported data).



5.1.2.5 Cautions in applying stock quality results

Limitations are inherent in stock quality assessment, depending on time of testing and the seedling morphological and physiological attributes that are measured (Puttonen 1989*a*, 1997). These limitations influence test result usage. To define field performance, morphological and physiological attributes need to be tested just prior to field establishment. This provides information on seedling initial field performance capability. However, spruce seedling inherent stress resistance changes as seedlings grow and follow the normal seasonal phenological cycle (Section 3.9). These patterns of stress resistance also change as seedlings are exposed to field site environmental conditions. Any testing procedure is just a "snapshot" of a single point in time along this seasonal pattern, making it difficult to accurately forecast all future seasonal patterns. Thus, the capability of these stock quality measurements to forecast seedling field performance potential is limited to a time frame that spans into the first growing season on a reforestation site.

Expression of seedling performance is largely regulated by reforestation site conditions. Stock quality assessment results may not always match field site performance, because it is difficult to simulate all possible combinations of stress (i.e., duration, timing, intensity, frequency) that occur under actual field site environmental conditions. Field performance potential testing programs can be applied to seedlings under projected field site environmental conditions. However, it must be recognized that any stock quality assessment program only provides information that forecasts, not predicts, actual seedling field performance.

When conducting any type of stock quality assessment procedure, one must recognize that differences in test results can occur due to species, genetic variation of seedlots (Section 4), variability in nursery culture, storage regimes, time of planting, and variability in testing conditions. Separate testing standards need to be developed for seedlings produced from various combinations of seedlot selections and nursery cultural decisions. Seedling users also have to be aware that the mishandling of stock during transport to planting sites, improper planting procedures, and unpredictability of field site environmental conditions can all influence how test results conducted prior to field planting match up with initial seedling survival and (or) field performance. Results derived from stock quality testing are only as good as the quality of operational procedures used in the overall forest regeneration program.

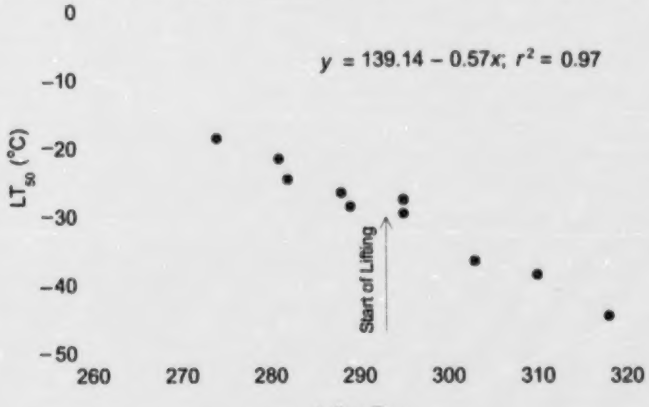
5.1.3 Nursery overwintering

Seedlings that are fall-lifted and stored throughout the winter for spring planting are either held outdoors, or stored in coolers or freezers. Successful application of this practice requires understanding how spruce seedlings change in relation to their dormancy cycle and physiological patterns (Section 3.9). This section describes how spruce seedlings develop the desired attributes required for fall lifting, so lifting for placement into storage can be properly timed. The effects of storage on seedling performance and seedling response after storage are also reviewed in this section. Readers interested in an extensive review on the practice of frozen storage are referred to Camm et al. (1994).

Nursery cultural practices that manipulate the photoperiod, drought, or nutritional balance affect the fall acclimation of spruce seedlings in the nursery. These environmental parameters are used to cause growth cessation and the development of dormancy (Section 5.1.1). As stated previously, the physiological basis behind nursery cultural practices that harden spruce seedlings is to trigger budset and the development of dormancy during the late summer and fall (based on physiological concepts discussed in Sections 2.5 and 3.9). With conifers, an indication of vegetative maturity is a point in time when there is an end to the shoot elongation phase and the initiation of over-winter buds (Burr 1990). After budset, fall acclimation of spruce occurs under normal conditions of decreasing day length and lower seasonal temperatures. This fall acclimation period is characterized by a total absence of shoot growth, a decrease in DBB_t to a low level, a rapid increase in freezing tolerance, and an initial decrease and then increase in root growth, indicating that spruce seedlings are at or near the end of rest (Section 3.9).

The best time to lift and store spruce seedlings is when they are at or near the end of rest, thereby ensuring the highest stress resistance, freezing tolerance, and root growth for improved growth and survival on a reforestation site during the upcoming growing season (Burr 1990; Ritchie and Tanaka 1990). Throughout Canada, seedlings are lifted in the fall only after they are able to survive a defined freezing temperature. The underlying principle requiring spruce seedlings to be tolerant of a −18°C freezing test, in British Columbia, before placement in storage, is that the development of freezing tolerance occurs in parallel with other phenological and physiological events that occur as spruce seedlings reach the end of rest (Burdett and Simpson 1984) (Section 3.9). Spruce seedlings that have passed the −18°C freezing test before being placed in storage have been shown to have the best survival and field performance capability during the next growing season (Simpson 1990). This same principle is applied in Ontario, where container-grown spruce seedlings are required to have a low index of injury after testing for freezing tolerance (i.e., ≤10% shoot injury after freezing to −40°C) before stock is placed in storage (Colombo 1997). In the United States, models of cold hardening in the fall have been developed for conifer species in order to decide when to begin the lifting of stock for frozen storage (Tinus 1996) (Fig. 5.1.3*a*). These models may make it possible to take just a few freezing test

Fig. 5.1.3*a*. Regression model of freezing tolerance for white spruce versus day of the year for 1996 (Tinus and Burr 1997). The arrow indicates the date when operational lifting began; based on an LT_{50} of −30°C that corresponds with good field survival (i.e., >70%) of frozen-stored bare-root seedlings planted in the next growing season.



measurements early in the season and project the rate of hardening (i.e., benchmarked to the LT_{50} temperature of –30°C) to determine the date when seedlings are ready to lift.

Another approach that is used in determining when to lift seedlings for storage is measurement of the dry weight fraction of seedling shoots. The use of this measurement approach is based on the fact that an increase in dry weight fraction is one of the physiological mechanisms that spruce species use to tolerate freezing temperatures (Section 2.4). Dry weight fraction increases in the fall in a predictable manner in spruce species (Colombo 1990; Calmé et al. 1993; Binnie et al. 1994). Since this fall pattern of increasing dry weight fraction reflects increased freezing tolerance, it is now used routinely by Scandinavian conifer seedling nurseries to determine when to begin lifting (Anders Mattsson, personal communication), with a dry weight fraction of ≥0.31 defining the optimum lifting dates (cf. Calmé et al. 1993).

Measurement of chlorophyll fluorescence is another testing approach that has recently been used for determining when to lift seedlings for storage. The measurement of chlorophyll fluorescence provides an indirect measure of the activity of the photochemical light reactions within the photosynthetic process (Section 2.2.3). During the fall, there is a seasonal inactivation of the photosynthetic process (Sections 3.3.1 and 3.9). A number of studies have found that fluorescence measurements parallel the increase in freezing tolerance and the development of dormancy in interior spruce seedlings during the fall acclimation process (Vidaver et al. 1989; Binnie et al. 1994; Binder and Fielder 1996*a*, 1996*b*). The fluorescence measurement procedure enables a large number of measurements to be taken in a short time. This efficiency in data acquisition has led to the speculation that the testing procedure could be used either as a viable alternative to, or in conjunction with, freezing tolerance testing as a means of determining the optimum time to lift seedlings for storage (Vidaver et al. 1991).

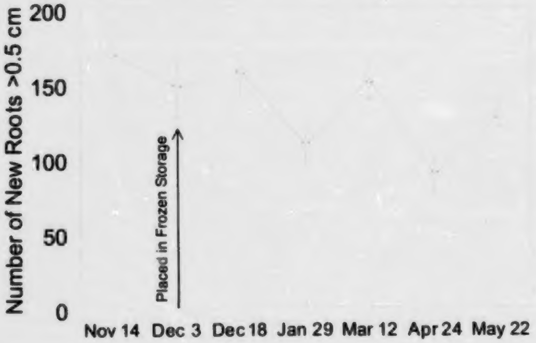
Chlorophyll fluorescence measurements do not always appear to be a reliable indicator of the level of dormancy and freezing tolerance in spruce seedlings (Devisscher et al. 1995). Because changes in photosynthetic capacity, development of dormancy, root growth, stress resistance, and freezing tolerance all occur in a parallel during fall acclimation, there are instances when measurement of one of these attributes does not coincide with the fall development pattern of the other attributes. While fall inactivation of the photosynthetic process and a general trend of fall acclimation can be measured by the chlorophyll fluorescence process, it is recommended that a final testing by the standard freezing test still be required before spruce seedlings are placed in storage.

Seedlings are usually placed in frozen storage at –2°C and are held for periods of 4–6 months. In certain instances, Sitka spruce seedlings are placed in cold storage at 0.5°C and can be held for up to 6 months (Cannell et al. 1990). Recent work has also found that long-term storage of up to 7 months of bare-root white spruce seedlings at a temperature as low as –6°C maintains seedlings with desirable stress resistance characteristics (Wang and Zwiazek 1999*b*). If bare-root

(Ritchie et al. 1985; Cannell et al. 1990) or container-grown (Simpson 1990; Grossnickle et al. 1994) spruce seedlings are placed into storage in a state of maximum stress resistance, they can maintain their physiological quality throughout the storage period. However, it must be realized that the seedlings are still physiologically active, although at a low level, and they keep changing throughout the storage period.

The ability of frozen-stored spruce seedlings to grow new roots can be maintained (Ritchie et al. 1985; Chomba et al. 1993) or it can decline (Ritchie et al. 1985; Camm and Harper 1991). Cold-stored Sitka spruce seedlings also maintained a high root growth capacity during long-term storage (Cannell et al. 1990). The pattern of root growth capacity for frozen-stored interior spruce seedlings is shown in Fig. 5.1.3*b*. Declining root growth may indicate seedlings are shifting priority emphasis from root to shoot growth and that extended storage may shift the natural sequence of next-season growth events (Camm et al. 1994). Declining root growth after extended storage may also mean an improper timing of the lifting period (Ritchie et al. 1985). Dormancy development in the fall can be altered by mid- to late-fall warming events (Section 2.5), which may alter the fall acclimation process of spruce seedlings (described in Section 3.9). This could result in the improper timing of the fall lifting period. There has also been some speculation that a decline in root growth may be due to a depletion of carbohydrate reserves during storage (Marshall 1985). The depletion of carbohydrates in frozen-stored black spruce seedlings was reported to correspond with the decline in the capability of the seedlings to grow new roots after extended storage (Kim et al. 1997). This variability in root growth after storage indicates that the previous season nursery cultural practices, fall acclimation environmental conditions, and length of storage can affect the ability of frozen-stored spruce seedlings to grow roots the following spring. Spruce seedlings that are lifted and stored properly have the capability to quickly respond to field conditions after planting. For example, root carbohydrate levels can increase quite rapidly after the planting of frozen-stored white spruce seedlings in the spring, indicating that a rapid increase in photosynthesis after planting (see below) can result in a

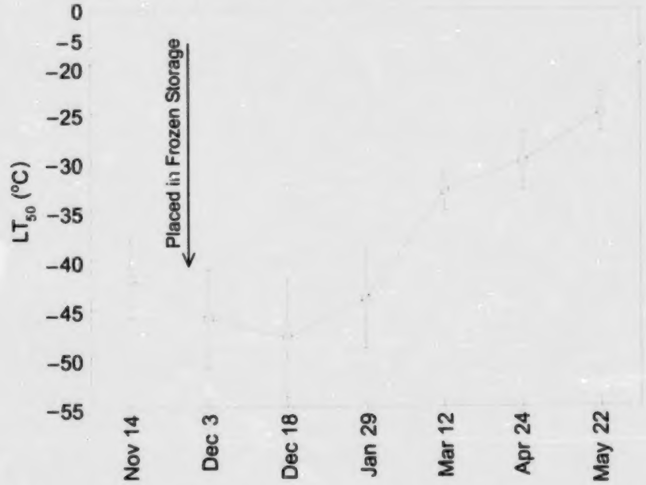
Fig. 5.1.3*b*. Change in root growth ($N = 24$: mean + SE) of interior spruce seedlings during frozen (–2°C) storage (adapted from Grossnickle et al. 1994).



translocation of carbohydrates from the shoots to the roots (Wang and Zwiazek 1999*c*). Root growth is important in newly planted seedlings to reduce the potential for planting stress (Section 5.3). Storage conditions should allow seedlings to maintain physiological integrity and thus a potential for high root growth capacity to improve chances of successful seedling establishment.

While in frozen storage, spruce seedlings can lose up to one-half of the freezing tolerance developed during the fall. This partial loss of freezing tolerance during storage is reported for frozen-stored containerized interior spruce (Fig. 5.1.3*c*) and Norway spruce (Lindström and Stattin 1994), and bare-root interior spruce (Ritchie et al. 1985) and cold-stored Sitka spruce (Cannell et al. 1990). The loss of normal seasonal light and temperature cues, and a decrease in carbohydrate reserves due to a continued low level of respiration, have been hypothesized as reasons for the decrease in freezing tolerance during storage (Ritchie 1986). Spruce seedlings are reported to have low levels of respiration rates in cold storage (Cannell et al. 1990) or frozen storage (van den Driessche 1979). In addition, a number of studies have found that carbohydrate reserves decline in stored spruce seedlings (Ronco 1973; Ericsson et al. 1983; Chomba et al. 1993; Jiang et al. 1994; Kim et al. 1997; Wang and Zwiazek 1999*b*). The loss of carbohydrate reserves in frozen conifer seedlings can cause a loss in freezing tolerance (Ögren 1997; Ögren et al. 1997), and this may be the reason for the decline in freezing tolerance of spruce seedlings while in frozen storage. However, it must be recognized that freezer storage seems to be a more viable alternative than outdoor storage. For example, freezer-stored Norway spruce seedlings retained a greater level of freezing tolerance in the spring, compared to seedlings that were stored outdoors (Lindström and Sattin 1994). Even though there is a

Fig. 5.1.3c. Change in freezing tolerance (measured by the freezing temperature resulting in 50% needle electrolyte leakage, LT_{50}) of interior spruce seedlings during frozen (–2°C) storage (adapted from Grossnickle et al. 1994).



loss of freezing tolerance during storage, this seems to be a typical phenomenon in the overwintering process of spruce seedlings (Section 3.7).

Spruce seedlings are normally packaged in plastic lined bags and then placed in wax-coated cardboard boxes to maintain a humid environment. Spruce seedlings that are frozen-stored under these conditions can have a 10% loss in seedling water content over a 5–7-month storage period, although this has no effect on seedling survival after field planting (Lefevre et al. 1991). This is probably due to the fact that spruce seedlings have a high degree of drought tolerance (Section 2.1.1) and drought avoidance (Section 5.1.4.1) capability during the winter period, enabling them to withstand mild levels of desiccation during frozen storage. However, severe desiccation during storage can cause a reduction in spruce seedling root growth capacity (Deans et al. 1990), which can increase the potential for planting stress in newly planted seedlings.

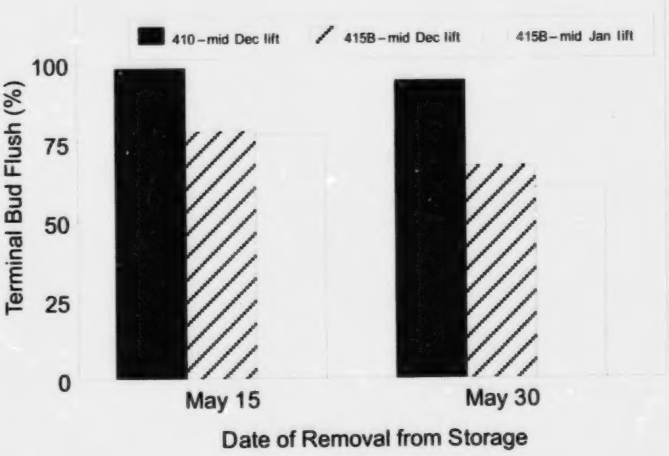
The alternative to overwintering of spruce seedlings in frozen storage for use in the spring planting program is outdoor winter storage. This practice has a number of drawbacks that limit its use within operational regeneration programs. First, the over-winter, outdoor storage of seedlings in containers can result in seedling exposure to extremely low temperatures when there is no snow cover. As already discussed, spruce seedling shoot systems develop a level of freezing tolerance that is easily able to withstand low temperatures (Sections 3.7.1 and 3.7.2). However, the exposure of the root systems of containerized seedlings to these low temperatures can result in damage because root systems of spruce seedlings are only able to tolerate freezing temperatures as low as ~–25°C (Section 3.7.2). Container-grown spruce seedlings that were stored over winter in an outdoor compound had reduced shoot and root growth the following spring, with greater reduction in growth, corresponding to lower root temperature (Lindström 1986). Field growth of seedlings can be affected for several years after root systems are damaged by freezing (Bigras 1998). Second, the over-winter, outdoor storage of seedlings in containers exposes the seedling shoot systems to winter desiccation. Seedling shoot systems are exposed to winter desiccation under conditions of frozen soil with bright sun and dry air. Under these environmental conditions, water stress occurs because seedling shoots are exposed to evaporative conditions, allowing a small amount of shoot transpiration to occur even though they cannot extract water from the frozen container soil plug (Section 3.7.5).

If seedlings are stored over winter in an outdoor compound, it is recommended that the containers be placed on the ground. This reduces the potential for low root temperatures (Lindström 1986). However, low root temperatures can still occur within the container soil plug if there is not adequate snow cover. In this case, other materials have been found to be somewhat effective at mitigating low root temperatures and protecting the shoot systems from winter desiccation. These include wood shavings (Aubin 1974), peat (Tinus 1982), straw (Gibbons 1983), thermoblankets, or plastic sheets (Gouin 1980), and Styrofoam® insulating blankets (Whaley and Buse 1994).

Dormancy of spruce seedlings coming out of storage can only be reversed if they are exposed to a series of environmental cues (i.e., warm temperatures and springtime photoperiods) that move them into an active growth phase (Section 2.5). After removal from storage, spruce seedlings usually require exposure to only 200–500 thermal hours (>5°C) before budbreak occurs (Ritchie et al. 1985; Cannell et al. 1990; Colombo 1990; Camm and Harper 1991; Grossnickle et al. 1994; Kim et al. 1997; Wang and Zwiazek 1999*b*). In contrast, on a field site, spruce seedlings can require 1300 thermal hours for budbreak (Section 4.3). Handling of seedlings in the nursery in a way that differs from normal field seasonal patterns (e.g., nursery cultural practices that alter the photoperiod, water and nutrient availability, lifting and placement of seedlings into dark cold storage or frozen storage) can alter the springtime budbreak response to environmental cues after the dormant period (Lavender 1991). As a result, spruce seedling budbreak patterns after removal from storage may or may not reflect the budbreak pattern of natural spruce seedlings.

An interesting phenomenon that has also been detected is the potential for a decrease in the number of spruce seedlings that break bud after removal from frozen storage. This trend continues the longer seedlings are left in storage (Fig. 5.1.3*d*). In addition, in certain years, the entire population of seedlings can show a reduced capability to break bud. This is not tied just to the date of lifting. Anatomical assessment of terminal buds for damaged frozen-stored interior spruce seedlings found abnormalities in both the bud-scale complex and the preformed shoot (MacDonald 1997). MacDonald (1997) speculated that this abnormal bud development may be due to water stress or a boron deficiency. Boron deficiency is known to limit bud development in spruce (Table 2.3.3). Another

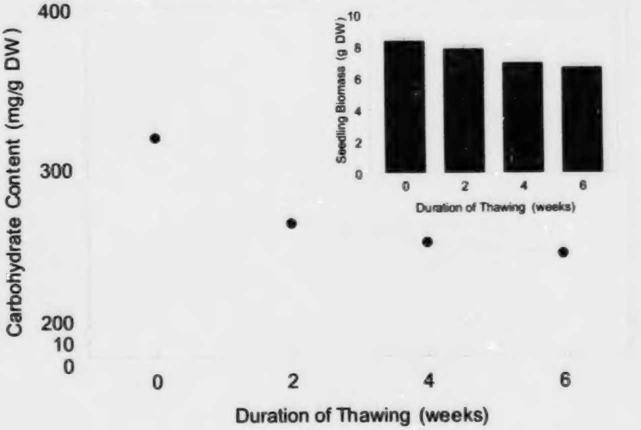
Fig. 5.1.3*d*. The percentage of container-grown (i.e., 410 of 415B designates the Styroblock® container size) interior spruce seedlings ($N = 25$), showing terminal bud flush just after removal from frozen (–2°C) storage (Grossnickle and Folk, unreported data).



possible physiological explanation for this phenomenon is that desiccation causes damage to the terminal buds as loss in seedling water content occurs over time in storage. This may occur when the lifted spruce seedlings have not developed the proper level of drought hardiness to withstand desiccation during storage. Spruce seedlings that do not have an adequate reduction in shoot water content going into storage can have greater needle damage after removal from storage (Colombo 1990). Spruce seedlings develop frost hardiness (Section 2.4) and drought hardiness (Section 2.1.1) in the fall, and this is due, in part, to the decline in shoot water content. This occurs as cell walls thicken, the secondary xylem lignifies, and proteins and sugars in the cytoplasm increase (Levitt 1980). Seedlings that do not develop a proper level of hardiness before being lifted and placed in storage may not be able to withstand any subsequent water loss during storage without bud damage. One must keep in mind that spring-planted seedlings have a growth pattern that allows them to occupy the site through the development of their shoot system during the first growing season on the reforestation site (Sections 5.1.4.1 and 5.4.1.3). Bud damage leads to a lack of terminal buds flushing and shoot development during the first year, negating one of the primary reasons for using this stock type.

The currently recommended practice for thawing frozen-stored seedlings is to remove seedlings from storage and slowly thaw at low temperatures (2–3°C) in the dark, or low light, over a 2-week period (Fraser et al. 1990). Thawing interior spruce seedlings under these conditions can result in a decline in total carbohydrate content (Fig. 5.1.3*e*), a loss of freezing tolerance, and drought tolerance (Silim and Guy 1997). Thawing for periods beyond 2 weeks has resulted in a further decline in these physiological attributes. Previous discussion has indicated that both drought tolerance (Section 2.1.1) and freezing tolerance (Section 2.4)

Fig. 5.1.3*e*. The change in carbohydrate content during the thawing period of interior spruce seedlings after removal from frozen storage (Silim and Guy 1997). The insert figure shows the change in subsequent growth over the first growing season after planting, in relation to various lengths of thawing frozen-stored seedlings.

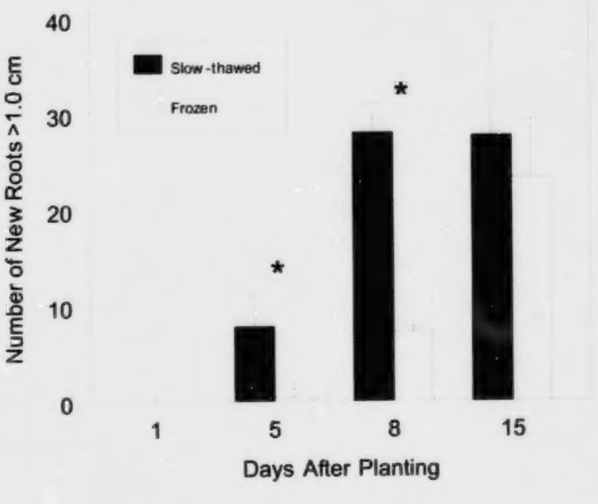


of spruce seedlings are related to the carbohydrate reserves of the seedlings. The use of an extended thawing period also results in a decrease in spruce seedling growth over the first growing season (Fig. 5.1.3*e*). Any condition that substantially reduces the carbohydrate reserves of conifer seedlings (e.g., storage practices) can reduce the growth capability of the seedlings (Marshall 1985). Silim and Guy (1997) recommend thawing frozen-stored seedlings for the shortest time that is feasible, as it results in seedlings of the highest physiological quality for subsequent field performance.

Planting spruce seedlings with either frozen container plugs (Kooistra and Bakker 1999) or with container plugs that were rapidly thawed (1–2 days in the dark, or low light) until the ice was gone (Camm et al. 1995) has no deleterious effects on their overall physiological performance. Camm and associates (1995) found that even though initial root growth of frozen-planted seedlings was less than slow-thawed seedlings, all seedlings had comparable root development 15 days after planting (Fig. 5.1.3*f*). In addition, rapid thawing practices had no subsequent effect on morphological development over the first growing season (Camm et al. 1995; Kooistra and Bakker 1999). This led Camm and associates (1995) to speculate that the currently used extended poststorage thawing practice may not be necessary. The use of the rapid thawing process of frozen-stored seedlings is currently being practiced in some reforestation programs throughout Canada (S. Colombo, personal communication).

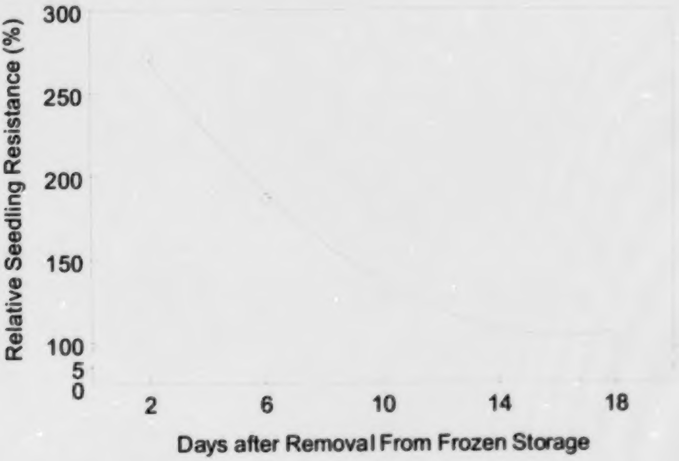
Seedlings require time to resume normal physiological responses after removal from storage and planting. Both g_{wv} (Grossnickle and Blake 1985; Grossnickle 1987; Harper and Camm 1993; Wang and Zwiazek 1999*b*) and P_{n} (Camm et al. 1991; Camm and Lavender 1993; Camm et al. 1995; Wang and

Fig. 5.1.3*f*. Root growth after planting slowly thawed or frozen white spruce seedlings (adapted from Camm et al. 1995). Note: the * indicates that the pairs differed at p <0.05 as determined by a t-test.



Zwiazek 1999*b*) for frozen-stored spruce seedlings are comparable to actively growing seedlings after approximately 1 week of time out of storage. Frozen-stored white spruce seedlings initially have a high resistance to water flow through the plant, especially at low soil temperatures just after removal from storage (Fig. 5.1.3*g*). This high level of resistance to water flow through frozen-stored spruce seedlings is due to the suberized state of their root systems (Section 2.1.2). The high resistance to water flow in frozen-stored spruce seedlings can create water stress during the initial days after planting, even when soil water is available (Camm et al. 1995). The initially high water flow resistance (Grossnickle and Blake 1985; Grossnickle 1987, 1988*a*) and water stress (Camm et al. 1995) decrease with time out of storage as spruce seedlings roots grow into the surrounding soil.

Fig. 5.1.3g. Change in relative resistance to water movement through white spruce seedlings (at 10°C soil temperature and optimum soil water, and relative to seedlings measured on day 18 that had some white roots) after removal from frozen (–2°C) storage (adapted from Grossnickle and Blake 1985).



5.1.4 Container-grown stock type characterization

Northern spruce species are produced as both container-grown and bare-root stock types throughout the world. By the early 1990s, over 90% of the conifer seedling production in British Columbia and over 75% of all conifer seedlings in Canada were produced as container-grown seedlings (Arnott 1992). This section focuses on the range of both physiological and morphological attributes of spruce stock types currently being produced for planting in British Columbia. The intent is to give readers an appreciation of what can be created within a containerized nursery program growing spruce seedlings.

The Styroblock® container system was developed during the 1970s and is currently the most popular container system used to grow conifer seedlings in British Columbia (Arnott 1992). Stock type characterization of spruce seedlings described in this section primarily pertains to container-grown seedlings produced within this Styroblock® container system. Section 5.1.4.1 addresses the performance of spring-planted versus summer-planted stock types, while Section 5.1.4.2 examines the performance characteristics of different size stock types. The initial performance of spruce seedlings in the field is related to their stock type. Performance is dependent upon the inherent growth potential of a stock type and can be defined by performance potential testing within a stock quality assessment program (Section 5.1.2.4). The following sections describe the stock quality attributes of currently produced stock types.

Containerized spruce seedlings can also be produced through the vegetative propagation systems of rooted cuttings and somatic embryogenesis tissue culture. These vegetative propagation technologies provide the opportunity to capture the additional genetic gains produced by tree improvement programs and can be used for bulking up the most elite, full-sib families. Section 5.4.1.3 briefly discusses the current developments of these propagation technologies for spruce forest regeneration programs.

5.1.4.1 Spring- versus summer-planted seedlings

This section provides a representation of performance potential attributes inherent in spruce containerized stock types commonly used during the spring and summer planting seasons. The performance of stock types used in the spring and summer planting program are also examined, in a later section, over two growing seasons in order to define how they become established on reforestation sites (Section 5.4.1.3). Stock types have their greatest effect on performance as seedlings become established and start to grow on the reforestation site. Each stock type has a specific growth pattern and level of stress resistance which affect physiological response and morphological development on a reforestation site. Spring-planted seedlings develop both the shoot and root systems during the first growing season. In contrast, summer-planted seedlings only develop root systems during the first growing season; these seedlings' first shoots elongate during the second growing season.

Morphological characterization of containerized stock types provides insight into the balance of a seedling. The 2+0 stock type has an overall larger shoot system than the other stock types due to the additional period of time for development in the nursery (Table 5.1.4.1). All stock types have morphological balance of their shoots (i.e., height to diameter ratio) as well as between their shoot and root. The 2+0 seedlings intended for the summer planting program have a larger shoot to root ratio, which is reflective of a larger shoot system development over two growing seasons. Root system development was comparable between all of the stock types, indicating that container cavity size limited continued root development during the second nursery growing season. Both 1+0 stock types have a similar number of lateral branches, although seedlings slated for summer planting have ~50% more buds along the shoots, compared to seedlings used in spring planting. The 2+0 stock type has fewer lateral branches than both 1+0 stock types, although it has a number of buds along the shoots comparable to the 1+0

Table 5.1.4.1. Stock type characterization (N = 10–24, depending on test: mean ± SE) of interior spruce seedlings used in spring and summer planting programs in British Columbia. Characterization is based upon stock quality attributes for 1+0 seedlings grown in 415B (at 105 mL) containers and for 2+0 seedlings grown in 415D (at 170 mL) containers (Grossnickle and Folk, unreported data).

	Spring-planted seedling		Summer-planted seedling		
	Units of value		Units of value		
Attribute^a	1+0	Comments	1+0	2+0	Comments
Height	23.2 ± 2.1 cm	Above BCMoF target of 22.0^b	24.8 ± 0.9 cm	28.0 ± 1.4 cm	BCMoF target of 22.0 for 1+0 and target of 30 for 2+0^b
Diameter	3.5 ± 0.3 mm	At BCMoF target of 3.5^b	3.6 ± 0.3 mm	4.7 ± 0.2 mm	BCMoF target of 3.5 for 1+0 and above the minimum of 4.2 for 2+0^b
Height to diameter ratio	6.5 ± 0.3 cm mm^{-1}	Fits the accepted BCMoF target^b	6.9 ± 0.1 cm mm^{-1}	6.2 ± 0.3 cm mm^{-1}	Fits the accepted BCMoF target^b
Shoot dry weight	2.72 ± 0.3 g	—	2.3 ± 0.2 g	3.3 ± 0.2 g	—
Root dry weight	1.07 ± 0.12 g	Exceeds the accepted BCMoF target of 0.7 g^b	0.72 ± 0.1 g	1.0 ± 0.2 g	Fits the accepted BCMoF target of 0.7 g^b
Shoot to root ratio	2.9 ± 0.3 g	Good balance for drought avoidance^c	2.9 ± 0.2 g	3.5 ± 0.2 g	Good balance for drought avoidance^c
Number of branches	16 ± 1	Large number of branches	17 ± 1	10 ± 1	Large number of branches
Number of buds	23 ± 1	Sites for potential shoot growth	36 ± 3	34 ± 2	Sites for potential shoot growth
Needle primordia in the terminal bud	230 ± 20	High predetermined shoot growth potential	186 ± 12	251 ± 24	Good predetermined shoot growth potential
Budbreak	10–14 days after planting	Influences subsequent physiological response	Not until the next spring	Not until the next spring	Influences subsequent physiological response

Table 5.1.4.1 *(continued)*.

	Spring-planted seedling		Summer-planted seedling		
	Units of value		Units of value		
Attribute[a]	1+0	Comments	1+0	2+0	Comments
Root growth capacity, optimum	32.2 ± 4.1	Fits the accepted BCMoF target[d]	40.5 ± 3.2	31.3 ± 3.6	Fits the accepted BCMoF target[d]
Root growth capacity, low temperature (10°C)	1.2 ± 0.5	5% of optimum RGC	—	—	—
Root growth capacity, after drought (–2.5 MPa)	—	—	28.2 ± 2.3	23.0 ± 7.1	70% of optimum RGC
Freezing tolerance at planting (II[f] at –6°C)	11 ± 5%	Freezing tolerance 4 weeks after planting: 44 ± 8%	45 ± 4%	43 ± 5%	Freezing tolerance 4 weeks after planting: 18–13 ± 1% for both stock types
Drought tolerance (Ψ_{dp})	–2.17 ± 0.24 MPa	Drought tolerance 4 weeks after planting: –1.48 ± 0.21 MPa	–1.6 ± 0.17 MPa	–1.6 ± 0.15 MPa	Drought tolerance 4 weeks after planting: –2.02 ± 0.22 MPa for the 1+0 stock type
Drought avoidance cuticular transpiration	0.41 + 0.08 mg $cm^{-2} s^{-1}$	Increases to 0.82 ± 0.06 mg $cm^{-2} s^{-1}$ after 4 weeks	0.92 + 0.12 mg $cm^{-2} s^{-1}$	0.61 + 0.12 mg $cm^{-2} s^{-1}$	Decreases to 0.66 ± 0.06 mg $cm^{-2} s^{-1}$ after 4 weeks for the 1+0 stock type
P_n optimum (14-day avg.)	1.37 + 0.12 μmol $m^{-2} s^{-1}$	At 45% of summer-planted seedling	2.98 + 0.37 μmol $m^{-2} s^{-1}$	2.42 + 0.27 μmol $m^{-2} s^{-1}$	Comparable to actively growing seedlings at a similar light level

Table 5.1.4.1 (*concluded*).

	Spring-planted seedling		Summer-planted seedling		
	Units of value		Units of value		
Attribute[a]	1+0	Comments	1+0	2+0	Comments
P_n at low root temperature (10°C) (14-day avg.)	1.06 + 0.28 μmol $m^{-2} s^{-1}$	Drops to 77% of optimum	—	—	—
P_n after drought (−2.5 MPa)	—	—	1.62 + 0.24 μmol $m^{-2} s^{-1}$	1.08 + 0.37 μmol $m^{-2} s^{-1}$	Drops to between 45 and 60% of optimum, for both stock types, during recovery

[a] Description of attributes are found in Table 5.1.2.4.

[b] Scagel et al. 1993; BCMoF, British Columbia Ministry of Forests.

[c] Grossnickle and Major 1994*b*.

[d] Section 5.1.2.2.

[e] Index of freezing injury.

summer-planted stock type. The number of needle primordia found in the terminal bud of both 1+0 and 2+0 stock types ranged from 186 to 250. These buds are the sites for potential shoot growth after seedlings are planted. However, seedlings planted in the summer do not usually break bud, and thus they have no shoot growth during the first field season, while seedlings planted in the spring usually break bud after a period of 10–14 days.

Root growth depends upon the edaphic conditions of the testing procedure. In this example, all stock types have comparable ability to grow roots under optimum conditions (Table 5.1.4.1). Spring-planted seedlings can show a wide range in root growth capacity, and this may be related to lifting and storage practices (Section 5.1.3). In contrast, root growth capacity of summer-planted seedlings seems fairly comparable between years (Fig. 5.1.1.1) and stock types. When spring-planted seedlings are planted under low soil temperature, root growth is reduced (Table 5.1.4.1) (Section 3.5.1). This indicates that even seedlings with acceptable root growth capacity can have difficulty becoming established when soil temperatures are low in the spring (Section 1.2.1). Summer-planted seedlings show good root growth after drought stress and can develop an effective root system to ensure establishment of seedlings (Table 5.1.4.1). This is an important attribute for summer-planted seedlings.

Seedlings planted in the spring (usually around mid May) have a high level of stress resistance just after planting. This is reflected in high freezing tolerance, drought tolerance, and drought avoidance characterization (Table 5.1.4.1). As these seedlings break bud, stress resistance declines, and 4 weeks after planting (during late spring and early summer), seedlings are at a low level of stress resistance and are in their most rapid phase of shoot growth. This development pattern conforms with the typical seasonal cycle for spruce seedlings (Section 3.9) and is the period when there is the lowest potential for frost (Section 1.2.3) or drought on northern reforestation sites.

Seedlings planted in the summer (usually around mid July) have low stress resistance just after planting. Low levels of freezing tolerance, drought tolerance, and drought avoidance are typical of both 1+0 and 2+0 stock types (Table 5.1.4.1). Thus, these seedlings are potentially vulnerable to freezing or drought just after planting. The only attribute that varies between these stock types is that 2+0 seedlings have lower cuticular transpiration than 1+0 seedlings, which provides greater drought avoidance capability under field conditions when VPD is high (Section 1.3.2). After 4 weeks, summer-planted seedlings show an increase in freezing tolerance, drought tolerance, and drought avoidance. Summer-planted seedlings do not break bud during the first growing season, and the development of stress resistance is reflective of the normal late-summer development in spruce seedlings (Section 3.9).

Spruce seedlings coming out of storage usually have low gas exchange capacity (Section 5.1.3). This pattern is reflected in the lower P_n of spring, compared to summer, planted interior spruce seedlings (Table 5.1.4.1). Spring-planted seedlings have reduced gas exchange capacity (i.e., P_n reduced by 23%) under low root temperature, which is a normal phenomenon for spruce seedlings

(Section 3.5.1). Summer-planted seedlings have higher P_n than spring-planted seedlings, which is reflective of the high level of gas exchange capacity found during the summer (Section 3.9). Interestingly, the 1+0, compared to 2+0, summer-planted stock type has higher P_n. After drought, summer-planted seedlings have a 40–55% decrease in P_n, with this reduction in P_n reflective of the low drought tolerance, thus P_n recovery (Section 3.5.2.1). As with root growth, the response of P_n is sensitive to field edaphic conditions, which can limit the gas exchange of seedlings just after planting.

Spring- and summer-planted stock types have different growth patterns and levels of stress resistance at the time of planting, which affects their physiological response and morphological development. It also needs to be realized that the level of stress resistance changes quite rapidly within a month after seedlings are planted. Data presented for these interior spruce stock types are intended to represent the general trends in inherent performance capabilities. Absolute values for any individual attribute can change from year to year, depending upon nursery cultural practices (Section 5.1.1) and the genetic source (Section 4). Nevertheless, these general differences in field performance potential should be recognized when making stock type selections. This information should be used in conjunction with knowledge of the reforestation site environment to select the best stock type and timing for planting.

5.1.4.2 Seedlings of various sizes

Foresters are frequently confronted with the fact that on some reforestation sites, vegetation can shade newly planted seedlings, thus reducing field performance (Section 5.5). Another problem facing foresters is that field sites with limiting environmental conditions may restrict the performance of planting stock. A solution being considered to deal with these regeneration problems is the use of larger planting stock. It is assumed that larger planting stock has the inherent performance potential to compete with other vegetation and has greater stress resistance to handle environmentally limiting field site conditions. This section provides information on the performance potential attributes inherent in spruce containerized stock types that have a range in sizes commonly used during the summer planting season. Stock quality characterization just before planting describes the material and performance attributes defined in the stock quality assessment section (Section 5.1.2). The field performance for spruce seedlings of various sizes under reforestation sites conditions is described elsewhere (Section 5.4.1.4).

Morphological characterization provides information on the shoot and root structural differences between these stock types. Seedlings grown in large-volume container cavities have greater shoot and root size, but maintain a comparable balance within the shoot system (i.e., similar height to diameter ratios), and between the shoot and root system (i.e., similar shoot to root ratios) (Table 5.1.4.2). Other work has found that spruce seedlings grown in large-volume container cavities are taller, have larger root collar diameters, and

Table 5.1.4.2. Stock type characterization ($N = 10–24$, depending on test: mean ± SE) of interior spruce seedlings (2+0 stock from the same seedlot) produced in three container volumes for the summer planting program (Grossnickle and Folk, unreported data).

Attribute^a	415B^b	415D^b	615A^b	Comments
Height	24.2 ± 0.8 cm	29.7 ± 0.7 cm	33.3 ± 0.8 cm	Fits the accepted BCMoF target^c
Diameter	4.4 ± 0.1 mm	5.0 ± 0.1 mm	6.8 ± 0.2 mm	Fits the accepted BCMoF target^c
Height to diameter ratio	5.6 ± 0.2	6.0 ± 0.2	5.0 ± 0.2	Fits the accepted BCMoF target^c
Shoot dry weight	2.83 ± 0.13 g	4.45 ± 0.2 g	6.40 ± 0.3 g	—
Root dry weight	1.06 + 0.06 g	1.40 + 0.08 g	2.06 + 0.10 g	—
Shoot to root ratio	2.84 ± 0.1	3.4 ± 0.1	3.3 ± 0.1	Good balance for drought avoidance^d
Number of branches	18 ± 1	24 ± 2	33 ± 2	Capability to occupy more area within the planting spot
Number of buds	50 ± 2	67 ± 3	86 ± 3	Capability to occupy more area within the planting spot
Needle primordia in the terminal bud	193 ± 35	164 ± 36	147 ± 38	Good predetermined shoot growth potential
Root growth capacity, optimum	34 ± 3	35 ± 4	30 ± 3.8	Fits the accepted BCMoF target^e
Root growth capacity, low root temperature (10°C)	24.4 ± 2.5	23.4 ± 3.0	19 ± 2.8	60–70% of optimum RGC
Root growth capacity, after drought (–2.5 MPa)	54 ± 5	38 ± 4	58 ± 7	10–50% greater than optimum RGC
Freezing tolerance at planting (II^f at –6°C)	78 ± 6%	68 ± 5%	77 ± 5%	Comparable to actively growing seedlings (Section 3.7)
Drought tolerance (Ψ_{tlp})	–1.66 ± 0.15 MPa	–1.64 ± 0.09 MPa	–1.49 ± 0.11 MPa	Comparable to actively growing seedlings (Section 2.1.1)
Drought avoidance cuticular transpiration	435 ± 72 mg H_2O (g DW)$^{-1}$ h^{-1}	364 ± 42 mg H_2O (g DW)$^{-1}$ h^{-1}	415 ± 60 mg H_2O (g DW)$^{-1}$ h^{-1}	—

Table 5.1.4.2 (*concluded*).

Attribute[a]	415B[b]	415D[b]	615A[b]	Comments
P_n optimum	2.72 ± 0.24 µmol m^{-2} s^{-1}	2.68 ± 0.27 µmol m^{-2} s^{-1}	2.09 ± 0.32 µmol m^{-2} s^{-1}	Comparable to actively growing seedlings (Section 3.3)
P_n at low root temperature (10°C)	2.12 ± 0.29 µmol m^{-2} s^{-1}	1.49 ± 0.12 µmol m^{-2} s^{-1}	1.49 ± 0.17 µmol m^{-2} s^{-1}	55–80% of optimum
P_n after drought (–2.5 MPa)	2.01 ± 0.32 µmol m^{-2} s^{-1}	1.53 ± 0.18 µmol m^{-2} s^{-1}	1.36 ± 0.11 µmol m^{-2} s^{-1}	55–75% of optimum

[a] Description of attributes are found in Table 5.1.2.4.

[b] All stock types were grown in format 600 Styroblock® containers (Beaver Plastics Ltd.) in the following individual cavity volumes: 415B at 105 mL, 415D at 170 mL, and 615A at 340 mL.

[c] Scagel et al. 1993; BCMoF, British Columbia Ministry of Forests.

[d] Grossnickle and Major 1994*b*.

[e] Section 5.1.2.2.

[f] Index of freezing injury.

greater total shoot and root dry weights (Lamhamedi et al. 1997; Paterson 1997). In addition to having a taller shoot, seedlings grown in large-volume container cavities have a greater number of branches and buds, but no greater potential for predetermined terminal shoot growth after field planting (i.e., number of needle primordia found in the terminal bud). Thus, large-volume container cavities produce a larger seedling that occupies a greater area within the planting spot, without compromising structural balance.

Root growth in spruce seedlings is dependent upon edaphic conditions. Across all three testing environments, there was no relationship between seedlings grown over a range of container volume cavities and root growth (Table 5.1.4.2). Root growth of spruce seedlings usually shows a general trend of greater new root growth with a greater original root system size (Fig. 5.1.2.2*b*). Root growth of spruce seedlings also varies, depending upon whether the stock type was stored for a spring planting program or fresh-lifted for a summer planting program, the nursery cultural practices, and the genetic source (Section 5.1.2.2). Thus, a larger root system does not necessarily ensure a greater ability to grow roots.

Seedlings of all sizes have similar physiological performance and material stock quality attributes. Interior spruce seedlings grown over a range of container volume cavities had comparable freezing tolerance and drought tolerance or avoidance (Table 5.1.4.2). Photosynthetic capacity was also comparable between seedlings of various sizes over a range of environmental conditions. This indicates that producing a morphologically larger seedling does not confer any additional physiological performance and material stock quality attributes to enhance performance under optimum or limiting environmental conditions. If there is a benefit of a larger seedling in relation to physiological performance, it is that its greater foliar mass allows for greater seedling photosynthetic capacity. This capability could be critical in enhancing the ability to grow quickly and occupy site resources during establishment.

5.1.4.3 Vegetative propagation systems

Major advances have been made over the past 25 years in the development of operational vegetative propagation systems for conifer species used in plantation forestry programs. These propagation systems provide a means of bringing new genetic material into forestry programs through the capture of a greater proportion of the gain from additive and nonadditive genetic components inherent within a selected tree species (Libby and Rauter 1984). In addition, vegetative propagation systems provide a rapid means for incorporating genetic gain into forest plantation programs. The value-added traits that can be captured through these vegetative propagation systems are those that can be identified through any tree-breeding program and include yield, wood quality, and pest, disease, and stress resistance. Vegetative propagation systems also provide a method for multiplying superior families identified in tree improvement programs (Gupta and Grob 1995). Vegetative propagation systems that produce spruce stock types utilize two different approaches: rooted cuttings and somatic embryogenesis tissue culture technology. Spruce species appear to be amenable to both of these propagation technologies.

Rooted cutting technology is the most effective vegetative propagation system currently available for northern spruce species on an operational basis. The primary use of rooted cutting technology is for bulk production of genetically improved material by multiplying specific individuals that have desirable traits and for bulking scarce or valuable forest tree seed. A recent survey reported that over 65 million conifer cuttings are produced annually around the world, with this number growing rapidly (Ritchie 1991; Talbert et al. 1993). Small scale programs are ongoing for bulking up Norway spruce in Europe (~1 000 000 cuttings) and Scandinavia (~8 500 000 cuttings) (Ritchie 1991). In Great Britain and Ireland, programs have been developed for Sitka spruce (Blackwood 1989), producing ~5 000 000 cuttings annually (Ritchie 1991). In Canada, there are programs throughout the eastern provinces to produce black spruce cuttings (~4 000 000 cuttings) (Ritchie 1991), while only very small scale cuttings programs for operational trials are ongoing for Sitka, interior, and white spruces in the western provinces (D. Summers, personal communication).

Production of rooted cuttings is essentially a two-step process. First is the production of cutting donor plants, and second is the production of rooted cuttings. Donor plants can range from selected trees of wild populations to seedlings (seed) grown from genetically improved families under an intensive nursery cultural regime. Rooted cuttings of forest tree species are most successfully produced from juvenile portions of donor plants because these portions show good initiation of root primordia (reviewed by Hackett 1988). The maturation of donor plants is considered the most serious single factor limiting the utilization of clonal forestry in spruce species on a large scale (Roulund 1981). The two methods most frequently used to arrest maturation of cutting donor plants are serial propagation and hedging. Serial propagation involves the repeated propagation of cuttings from recently rooted cuttings. Serial propagation has been used in Norway spruces, and this approach has been effective in slowing, although not arresting, the maturation process of cutting donor plants (Kleinschmit and Schmidt 1977; St. Clair et al. 1985). Hedging involves the repeated pruning of the cutting donor plants and has been shown to provide spruce cuttings of an apparently more juvenile developmental state (e.g., Roulund 1975; van den Driessche 1983). The use of hedges to produce juvenile spruce cuttings is used in operational programs throughout the world, although in certain instances the maturation of hedges has resulted in the abandonment of this approach (Talbert et al. 1993). An alternative approach that has been used effectively to produce juvenile cuttings for spruce species is the use of seedling-origin hedges (Russell and Ferguson 1990). In this approach, the cutting donors are produced from seed originating from genetically improved families. Seedlings are grown under an intensive nursery culture regime, and newly developed shoots are pruned regularly to produce an average of 65 cuttings from each donor seedling. A program developed for black spruce uses a hybrid between serial propagation and hedging (Tousignant et al. 1996). Seedling-origin hedges are initially grown for 3 years under an intensive cultural regime in the nursery followed by 3 years in field-based hedge orchards. Cuttings are taken during each of the 6 years the stock plants are in production. The serial propagation of black spruce in this manner can produce an average cumulative yield of ~342 cuttings per plant over 6 years. Spruce cuttings from all donor plant origins are placed in a rooting environment (i.e., high humidity, high soil water, warm soils, and moderate light), allowed to develop roots (i.e., taking up to 3 months), and then treated as rising 1-year-old seedlings (Talbert et al. 1993). Readers are referred to Landis et al. (1999) for further information on operational procedures used to produce rooted cuttings.

Rooted cuttings produced from spruce species initially have a morphological form that differs from operationally produced zygotic seedlings. Rooted cuttings of Norway spruce are stockier than seedlings; rooted cuttings have a greater root collar diameter and shoot dry weight with a well-developed root system (Kleinschmit and Schmidt 1977). Rooted Norway spruce cuttings have a higher degree of plagiotropism when age of the donor plant increases or when cuttings are taken from higher branches on the donor plant (Roulund 1979). When rooted Norway spruce cuttings are produced from juvenile material, they have good height growth, free growth capability as well as an orthotropic growth form (i.e., vertical growth form), and a radial arrangement of needles and branches (Wühlisch 1984). Current nursery cultural practices allow for the manipulation of the growing environment regime to ensure that spruce rooted cuttings meet accepted morphological standards for a plantable stock type (Russell and Ferguson 1990). Field trials comparing rooted cuttings to seedlings for conifer species have shown no significant difference in survival and relative growth rates between these stock types (Talbert et al. 1993). Field trials with Norway spruce (Roulund 1974, 1977) and Sitka spruce (Roulund 1978; O'Reilly and Harper 1999) have shown that rooted cuttings have superior growth when compared to seedlings. The benefit of using rooted cuttings from material with improved genetic gain is born out in Norway spruce programs throughout Europe and Scandinavia. There, a 10–30% improvement in height and volume growth has been reported when rooted cuttings were compared to seedlings from standard seed sources (Bentzer 1993). The ability to capture the genetic gain from spruce tree improvement programs and to produce a good quality stock type has led to the successful integration of rooted cuttings into plantation forestry programs.

Somatic embryogenesis is a tissue culture method of asexual propagation. The term somatic refers to embryos developing asexually from vegetative (or somatic) tissue. This method has been used to some extent in forestry as a means of rapidly multiplying elite varieties or clones. In conifers, embryogenic cultures are induced from developing and (or) mature zygotic embryos or young germinants, although it has not been possible to induce cultures from older explants (Tautorus et al. 1991; Roberts et al. 1993). Thus, somatic embryogenesis fulfills a role similar to cuttings with respect to the multiplication of superior families.

Distinct from conventional cuttings, somatic embryogenesis offers the capability for long-term storage of germplasm through cryopreservation (Cyr et al. 1994; Park et al. 1998). Cryopreserved tissue can be regenerated, without a loss of juvenility, to allow for the development of somatic embryos from clones selected on the basis of superior performance in short- to long-term field trials. Through the application of bulk-handling techniques, somatic embryogenesis has the potential to become a cost-effective approach for the propagation of conifers (Sutton et al. 1993; Roberts et al. 1995).

Seedlings produced through somatic embryogenesis are now being integrated into plantation forestry programs throughout the world. A number of nursery and field trials are ongoing with spruce species (e.g., black: Adams et al. 1994, Klimaszewska 1995; Norway: Gupta et al. 1993, von Arnold et al. 1995; red: Isabel and Tremblay 1995). Recently, the program for interior spruce has developed to the point that somatic seedlings are annually being planted (~500 000 somatic seedlings) on reforestation sites on an operational basis (Grossnickle et al. 1996*c*). There are few programs, other than those on interior spruce, that have reported on growth and ecophysiological performance of somatic, compared to zygotic, seedlings in nursery and plantation trials (Grossnickle and Major 1994*a*, 1994*b*; Grossnickle et al. 1994). Thus, the following discussion focuses primarily on the performance of interior spruce somatic seedlings.

Stock quality testing of somatic interior spruce seedlings indicates that their performance is similar to zygotic seedlings under both cold (i.e., frost and low soil temperature) and drought (Grossnickle and Major 1994*a*) conditions. Interior spruce somatic seedlings have morphological development that meets conventional containerized stock type standards, although between-clone variability in morphological development is evident (Section 4.4.1). There have been previous reports of accelerated maturation in conifer plantlets produced in vitro via cotyledonary organogenesis tissue culture technology (Gupta et al. 1991). This early maturation can affect seedling performance through decreased growth rates, mature foliage and branching characteristics, and premature flowering. Recent work with red spruce found no evidence that somatic seedlings show any signs of accelerated maturation (Nsangou and Greenwood 1998). These reported findings indicate that there is a comparable quality between somatic and conventional seedlings.

Reforestation site trials were set up to test the field performance of interior spruce somatic seedlings in comparison to zygotic seedlings (Grossnickle and Major 1994*b*). These trials found comparable summer seasonal water relation patterns and gas exchange response patterns between stock types. Both stock types had comparable height, diameter, and root growth over two seasons. The survival rates of somatic and zygotic seedlings after two growing seasons were also similar. Thus, somatic seedlings demonstrate field performance that is desirable in a container-grown stock type for use in forest regeneration programs.

The use of tree improvement to enhance the genetic characteristics of planted seedlings is a forestry practice that consistently shows a return on investment by increasing yields obtained from planted forests. Northern spruce species have a wide range of genetic variation in physiological response and morphological development in relation to environmental conditions (Section 4). Ongoing tree improvement programs for spruce species are intended to capture superior performance traits and then incorporate these genetic gains into the operational reforestation program. The use of improved seed from seed orchards is the most readily used way of bringing genetic improvement to forest regeneration programs. For northern spruce species, both rooted cuttings and somatic embryogenesis tissue culture technologies can provide a means for vegetative multiplication of specific elite genotypes and to bulk up scarce elite families.

5.1.5 Handling

Handling practices can include any number of nursery cultural and forest regeneration operations. These operations include lifting, bundling, packing, nursery storage, shipping, onsite storage, and planting. Almost all plants and plant parts respond in some way to mechanical perturbation (Jaffe 1980). Thus, any improper handling practice can have an effect on the subsequent seedling performance (reviewed by McKay 1997). If these operations are conducted with care, their effects on seedling performance is minimal. However, if seedlings are treated in a rough manner, subsequent seedling performance is affected.

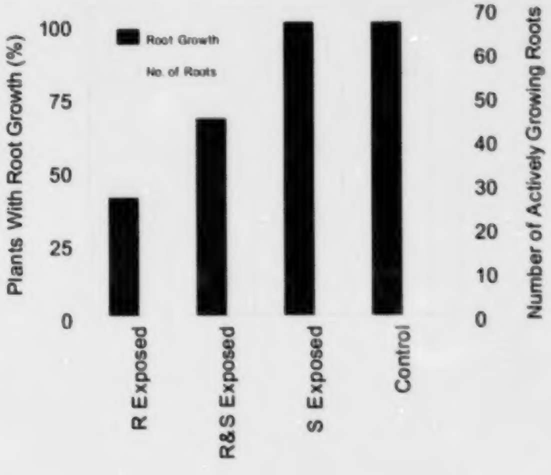
Rough handling of bare-root seedlings (i.e., dropping, bouncing, blows directly to the root system) during movement from the nursery to the field causes a depression in root growth (Tabbush 1986*a*; Deans et al. 1990; McKay et al. 1993; Stjernberg 1996, 1997) and height growth (Tabbush 1986*a*; Tabbush and Ray 1989; Sharpe et al. 1990; McKay et al. 1993; Stjernberg 1997) during the first growing season after field planting. In addition, this rough handling can cause a reduction in subsequent mycorrhizal development (Tabbush 1986*b*). Containerized seedlings have a greater capability to withstand rough handling. In a number of cases, rough handling had little effect on subsequent seedling root and shoot growth (Silim and Lavender 1991; Simpson et al. 1994; Stjernberg 1996, 1997). This led Stjernberg (1996, 1997) to speculate that the root-growing media plug acted as structure to minimize the effects of handling impacts on root systems of containerized seedlings.

Interestingly, the ability of spruce seedlings to withstand rough handling changes seasonally. Both bare-root (Deans et al. 1990; Yuyitung et al. 1994) and containerized (Lavender 1989; Silim and Lavender 1991) seedlings have a high resistance to handling stress when seedlings are inactive. Rough handling of container-grown white spruce seedlings had no effect on root growth of seedlings just removed from storage, while rough handling of freshly lifted seedlings used for summer planting decreased root growth (Lavender 1989). Thus, there is a lower level of resistance to handling stress in actively growing spring- and summer-planted seedlings. This pattern fits with the yearly growth cycle described for spruce seedlings, where late fall and winter are defined as the period of maximum stress resistance, while springtime and early summer is the period of lowest stress resistance (Section 3.9).

Lost in this debate on the effects of handling on seedling performance is whether normal handling practices that occur during a regeneration program influence the performance of spruce seedlings. Normal operational handling procedures seem to have no effect on the performance of containerized spruce seedlings (Stjernberg 1996). Stjernberg (1997) indicated that normal vehicle transportation caused only minor mechanical shocks, although small, all-terrain vehicle transportation at the planting site produced high amplitude mechanical shocks to the seedlings. All of the above evidence indicates that rough handling practices reduce the physiological quality and subsequent performance of spruce seedlings. Care must be taken to avoid unwarranted rough handling. Normal handling practices do not reduce the performance of container-grown spruce seedlings.

Improper handling practices on the field site just prior to planting can expose seedlings to drying. Any combination of increasing air temperature and decreasing relative humidity can increase the VPD level (Section 1.3.2), which can cause the drying of seedlings exposed to the air (Section 3.2). The effects of drying depend upon whether roots or shoots are exposed. It seems that the exposure of roots to air, compared to shoots, during the handling practice can cause a greater reduction in seedling performance as a result of seedling water stress (Coutts 1981). In this example, both the number of seedlings with active root growth and the number of actively growing roots on each seedling was less when roots, compared to shoots, had been exposed to the air (Fig. 5.1.5*a*). Other work has also confirmed that exposure of roots to the air causes water stress and impairs the subsequent root growth of seedlings (Deans et al. 1990; McKay 1994). Exposure of spruce seedlings to root desiccation just prior to planting can also

Fig. 5.1.5*a*. Effects of exposure treatment (i.e., exposed to the air until shoot Ψ decreased to –2.0 MPa) on the root activity of bare-root Sitka spruce seedlings (adapted from Coutts 1981). Treatment abbreviations are as follows: R, root; S, shoot; R&S, root and shoot exposure to drought.



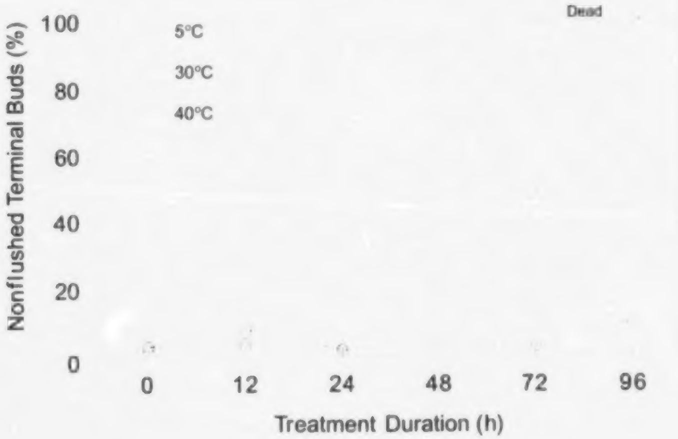
lead to reduced survival and shoot growth after planting (Tabbush 1987; Nelson and Ray 1990; McKay and White 1997). Spruce seedling root systems are susceptible to damage from exposure to dry air through improper handling practices.

Once seedlings have been exposed to desiccation, there is a limited amount of revitalization possible. Rewetting of spruce seedling roots after desiccation did not improve subsequent survival and growth (Tabbush 1987). In some instances, this handling stress can be mitigated by the use of root dips that seem to limit water loss through exposed root systems (Section 5.1.1.5). Careful handling of seedlings during the planting process is necessary to minimize the potential for damage to seedlings exposed to water stress before planting.

There is the potential danger of exposure to high temperature during the transportation of seedlings to, and storage on, the field site. Long exposure to temperatures above 40°C can cause cellular damage, with the level of damage affected by the phenological state of the seedling (Section 3.3.2). Frozen-stored spruce seedlings can withstand up to 4 days of storage at 20°C without any effects on physiological integrity and subsequent field performance (Binder and Fielder 1995). However, shoot tissue of spruce seedlings starts to show cell damage after 24 h of exposure to 30°C and after just 4 h at 40°C (Binder and Fielder 1995). In this example, extended exposure to high temperatures (i.e., 30 and 40°C) caused a rapid reduction in the number of seedlings that flushed in the spring (Fig. 5.1.5*b*). Exposure to 35°C causes a reduction in interior spruce seedling functional integrity (measured by g_{wv} and root growth capacity) and subsequent survival and growth (Simpson et al. 1994).

Seedlings should be stored at temperatures close to 5°C during the transportation of seedlings to, and their storage on, the field site. Normal shipping of

Fig. 5.1.5*b*. Percent of nonflushed terminal buds of white spruce seedlings 28 days after planting following exposure to storage conditions at different temperatures (adapted from Binder and Fielder 1995).



seedlings to the field occurs in refrigerated trailers where temperatures are usually below 10°C (Dunsworth 1997; Stjernberg 1997). Occasionally, higher temperatures occur when seedlings are stored on site (Dunsworth 1997; Stjernberg 1997). Temperatures can rapidly rise to 40°C in storage containers on field sites (DeYoe et al. 1986). Thus, care must be taken to avoid handling situations that can expose seedlings to high temperatures prior to planting. These high temperatures can reduce field performance of spruce seedlings.

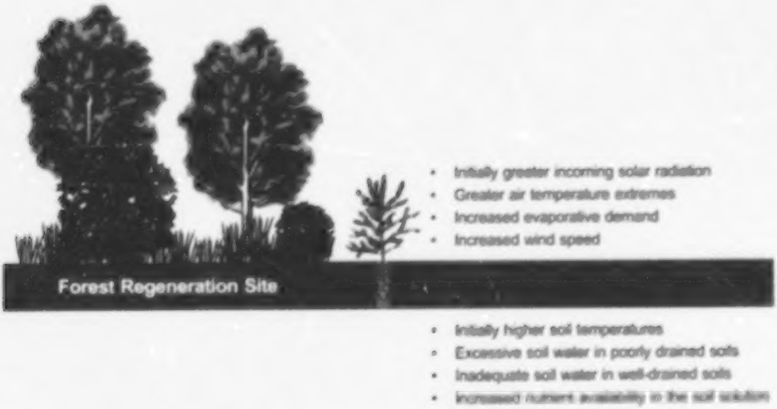
As described above, single incidents of improper handling (i.e., rough handling, desiccation, extreme temperatures) can reduce the field performance of seedlings. It must be recognized that reduced seedling performance can also result from damage due to repeated minor stress events, with each individual event not causing detectable damage. Rather, it is the accumulation of these minor stress events that reduce seedling performance. McKay (1997) theorizes that seedling damage due to desiccation and storage at low and ambient temperatures seems to be cumulative. On the other hand, mechanical stress associated with normal handling and transportation procedures were not sufficient to reduce the survival and growth of container-grown seedlings (Stjernberg 1997). Foresters must recognize that container-grown spruce seedlings are biological organisms that have seasonal cycles of tolerance to stress (Section 3.9). Care needs to be taken when handling seedlings during forest regeneration operations.

5.2 Planting spot location

Two major factors are considered when choosing planting spots for seedlings. First is the location in which a seedling is planted. After a major disturbance, horizontal and vertical heterogeneity is usually very high, although vertical heterogeneity is primarily present just near the soil surface due to the short stature of vegetation (Spies 1997). Selection of planting spots on these disturbed sites is generally dictated by slash, rocks, debris, depth of organic layer, natural seedlings, and competition across the site. This factor has a very strong influence on growth of the seedling. Second is the target density for the area to be reforested. Every reforestation program has a target for the number of seedlings that are planted for a given area. However, target densities should not be the overriding factor in determining the exact number of seedlings planted in a given area. Planting densities should be based upon the available microsites across the reforestation site.

The local climate broadly reflects regional climate, but microclimatic conditions may vary considerably, depending upon elevation, topography, and aspect. At the microclimate scale, forest canopy removal has a major effect on the radiation balance, which leads to changes in air temperature and relative humidity, thereby affecting VPD. Forest canopy removal also affects the water balance and fertility of the soil. Thus, the selection of a planting spot determines the microclimate surrounding a seedling (Fig. 5.2). The regeneration niche for boreal reforestation sites proposed by Margolis and Brand (1990) provides a generalization of the environmental conditions that seedlings are exposed to on a clear-cut site.

Fig. 5.2. Microsite environmental conditions of the planting spot on a northern latitude reforestation site that can influence the performance of planted spruce seedlings.


Initially greater incoming solar radiation
Greater air temperature extremes
Increased evaporative demand
Increased wind speed
Forest Regeneration Site
Initially higher soil temperatures
Excessive soil water in poorly drained soils
Inadequate soil water in well-drained soils
Increased nutrient availability in the soil solution

These include (*i*) high light intensity, (*ii*) high or low soil water availability, (*iii*) low to medium soil temperatures, (*iv*) high soil surface temperatures, (*v*) high vapor pressure deficits, (*vi*) high incidence of frost, (*vii*) high wind speeds, and (*viii*) high nutrient availability in the soil solution. Specific details on all of these environmental parameters as they relate to clear-cut reforestation sites have been previously described in Section 1. The environmental changes that occur with the use of a partial forest canopy retention system are discussed later in this treatise (Section 5.6). Foresters must recognize which of these site-specific environmental factors might limit seedling performance on each reforestation site, and they must make the selection of planting spots based on the best available planting microsites.

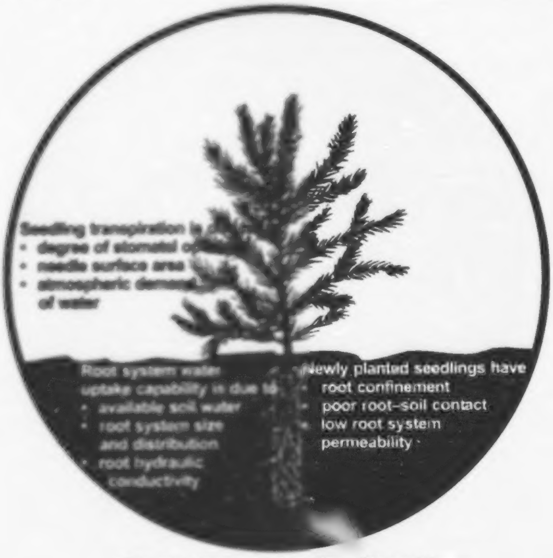
Environmental factors that determine the planting spot microsite also directly affect the physiological response of spruce seedlings (as described in Section 3). It is important to recognize that reforestation sites have ever-changing environmental conditions and that spruce seedling ecophysiological processes continually respond to these site conditions. Also, seedlings undergo many morphological and physiological changes during the annual cycle, which affects the degree of stress resistance (i.e., both tolerance and avoidance) to environmental conditions (Section 3.9). Field performance is also related to the inherent genetic variation in the physiological performance of spruce seedlings (Section 4). Foresters see the subsequent effect of this dynamic interaction between site environmental conditions and seedling physiological response as field survival and growth performance. Understanding the way in which these physiological processes affect spruce seedling field survival and growth can improve the forester's capability to make proper planting spot selection and additional silvicultural decisions that impact on plantation performance.

It is also critical to realize that the amount of space, both above- and below-ground, between competing vegetation and newly planted seedlings has a direct bearing on microclimate. Early seral stage species with a high level of overall physiological activity and growth are in direct competition with spruce seedlings within this reforestation site environment. Competing vegetation creates microclimates that are ever changing; over time this vegetation alters the environmental conditions of the planting spot (Section 5.5). Understanding the interaction between competing vegetation and the ecophysiological processes of newly planted spruce seedlings is paramount to the selection of desirable planting spots, thereby enhancing the potential for successful development of free-to-grow forest plantations.

5.3 Planting stress

Seedlings can be exposed to stress just after planting on a reforestation site. Stress occurs because reforestation sites can present extreme environmental conditions which alter site heat exchange processes and soil water relations (Miller 1983) (Sections 1.2 and 1.3) (Fig. 5). To ameliorate these conditions, seedlings require a continuous movement of water from absorbing roots to transpiring needles to maintain a proper water balance and ensure survival. The ability of a seedling to take up water is influenced by available soil water, root system size and distribution, root–soil contact, and root hydraulic conductivity (Fig. 5.3*a*) (Sections 1.3.1 and 2.1.2). Transpirational loss from the needles is determined by the degree of stomatal opening (g_{wv}), needle area, and the atmospheric demand for water (response to VPD, Section 3.2).

Fig. 5.3*a*. Descriptive representation of planting stress in spruce seedlings.

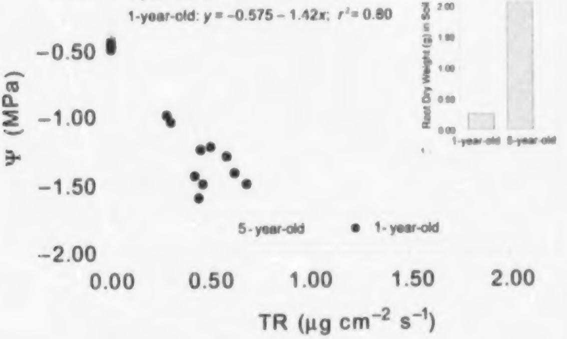

Seedling transpiration is
• degree of stomatal
• needle surface area
• atmospheric demand
of water
Root system water
uptake capability is due to
• available soil water
• root system size
and distribution
• root hydraulic
conductivity
Newly planted seedlings have
• root confinement
• poor root–soil contact
• low root system
permeability

Planting Stress = Seedling Water Stress

Typically newly planted seedlings have restricted root placement, poor root–soil contact, and (or) low root system permeability, which can limit water uptake from the soil (Kozlowski and Davies 1975; Burdett 1990). A lack of root development into the soil for newly planted interior spruce seedlings can result in increased seedling water stress (Draper et al. 1985). This occurs because newly planted seedlings, with little root development, have a higher resistance to water movement through the SPAC, which results in lower seedling Ψ at the same level of transpiration as older seedlings with well-developed root systems (Fig. 5.3*b*) (Bernier 1993). If sufficient root growth does not occur, spruce seedlings continue to be under water stress, and seedling mortality can occur (Hines and Long 1986). New root growth increases the capability of a seedling to access water from a greater soil volume. In addition, new roots can absorb greater amounts of water, thereby reducing the level of root resistance to water movement from the soil through the root and into the xylem (Section 2.1.2). A number of studies have shown that when root growth does occur in newly planted seedlings, an increase in daily seedling Ψ occurs, except under limiting environmental conditions, and seedling physiological processes begin to resume normal functionality (Sands 1984; Grossnickle and Reid 1984*b*; Carlson and Miller 1990; Brissette and Chambers 1992). The potential for damaging water stress levels is reduced as new root development occurs, thereby improving seedling establishment after planting.

Soil water content can also affect whether planting stress occurs in newly planted seedlings. Near-surface and root-zone soil water deficits can be a major constraint to spruce seedlings on boreal reforestation sites. Root-zone soil water deficits are the result of evaporation from the soil surface and transpiration from competing vegetation (Section 5.5.3). Planting stress can also occur in flooded soil conditions which restrict water uptake by seedlings (Section 3.5.2.2). Planting stress does not occur when newly planted seedlings are exposed to

Fig. 5.3*b*. The relationship between transpiration rate (TR) and shoot water potential (Ψ) for 1- and 5-year-old Engelmann spruce seedlings on an afforestation site. Insert figure represents the amount of seedling root growth out into the soil (adapted from Grossnickle and Reid 1984*b*).



conditions of abundant soil water and (or) low atmospheric evaporative demand. Under these conditions, new root development is not required because the existing root system is adequate to supply water to the shoot system to meet transpirational demand. Thus, various levels of soil water content have a direct influence on whether newly planted seedlings are exposed to water stress.

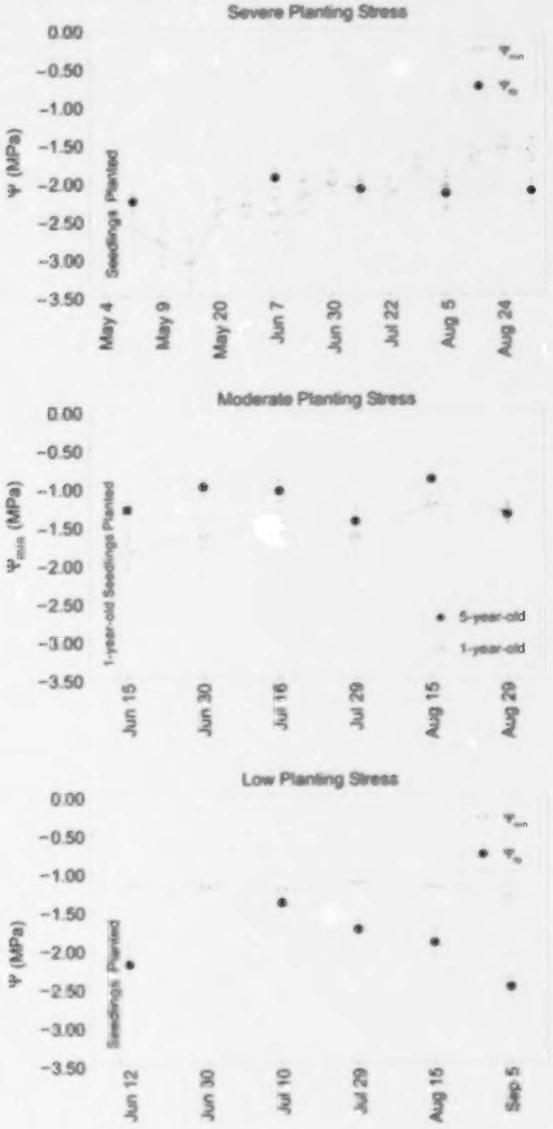
Planting stress can be affected by the hydraulic properties of the soil system. Soils that are high in organic matter content, within the rooting zone of newly planted seedlings, have an increase in soil porosity, a decrease in bulk density, and an increase in saturated hydraulic conductivity (Section 1.3.1). At soil water contents below saturation, however, soils of high organic matter content can have a decrease in unsaturated hydraulic conductivity (Hillel 1971), which reduces water movement to the roots. For example, Engelmann spruce seedlings planted in soils with high organic matter content had increased seedling water stress throughout the growing season (Grossnickle and Reid 1984*b*), which resulted in increased mortality (Grossnickle and Reid 1982). In this instance, successful establishment was affected by the hydraulic properties of the soil within the rooting zone.

Planting stress can occur at varying levels of intensity and for varying lengths of time, depending upon how spruce seedlings respond to planting. The following are three examples of planting stress that can occur in newly planted spruce seedlings.

Severe planting stress can be defined by a level of water stress severe enough to limit a major physiological process during most of the daylight period, although not severe enough to cause death (Section 2.1.3). Bare-root white spruce seedlings had very low Ψ during the first 3 weeks after planting ($\Psi_{min} < -2.50$ MPa) (Fig 5.3*c*). Initial root growth was detected on these seedlings after 2 weeks, resulting in an increase in daily Ψ_{min} levels (increased to between −2.0 and −2.5 MPa) (Grossnickle and Heikurinen 1989). However, during the first two-thirds of the growing season, Ψ_{min} was lower than or comparable to Ψ_{tlp}. This indicates that during midday, white spruce seedlings were at a level of water stress exceeding the turgor loss point, causing a reduction in physiological processes (Section 2.1.1). These seedlings had not yet developed enough of a root system to access sufficient soil water to meet the transpirational demands placed on the shoot systems. In the final third of the growing season, Ψ_{min} increased as enough root system development occurred, which allowed for sufficient water uptake to meet transpirational demands.

In moderate planting stress, recently planted seedlings are initially exposed to water stress which quickly disappears during the growing season. For example, containerized Engelmann spruce seedlings showed Ψ_{min} ranging between −1.5 and −2.0 MPa over the first month of the growing season (Fig. 5.3*c*). Initially, these recently planted seedlings had lower Ψ_{min} than seedlings growing for 5 years on the reforestation site. This was due to minimal root development during the first half of the growing season, coupled with high atmospheric evaporative demand and limited water in the upper portions of the soil profile

Fig. 5.3c. Examples of varying levels of water stress for newly planted spruce seedlings over a range of reforestation sites. Severe planting stress is represented by bare-root white spruce seedlings planted on a site in northern Ontario (adapted from Grossnickle 1988*b* and Grossnickle and Heikurinen 1989). Moderate planting stress is represented by container-grown Engelmann spruce seedlings planted on a site in Colorado (Grossnickle 1983). Low planting stress is represented by container-grown interior spruce seedlings planted on a site in central British Columbia (adapted from Grossnickle and Major 1994*b*). The parameters presented in the figure are minimum daytime shoot water potential (Ψ_{min}), measured between 1200 and 1330 h, and osmotic potential at turgor loss point (Ψ_{tlp}).



(Grossnickle and Reid 1984*b*). This limited water uptake from the soil resulted in greater resistance to water movement through the SPAC (Fig. 5.3*b*). By the second half of the growing season, Ψ_{min} was comparable to seedlings growing for 5 years on the reforestation site (Fig. 5.3*c*). This is because recently planted seedlings had developed sufficient roots to allow for adequate water uptake from the soil.

In low planting stress, recently planted seedlings are never exposed to severe water stress during the growing season. For example, interior spruce seedlings showed no indication of water stress (Ψ_{min} at –1.2 MPa) the first month after planting (Fig. 5.3*c*). This was due, in part, to access to soil water and low atmospheric evaporative demand throughout the early part of the growing season (Grossnickle and Major 1994*b*). By early July, the seedlings had enough root development to allow for sufficient water movement through the SPAC, even though soil water declined later in the growing season (Grossnickle and Major 1994*b*). Seedlings were exposed to water stress only in early July. This was due to seasonal changes in Ψ_{tlp}, rather than a decline in Ψ_{min}. Seasonal increases in Ψ_{tlp} occurred during the period of shoot growth and is a regular growing season phenomenon within the phenological cycle (Sections 2.1.1 and 3.9). During the shoot growth period, spruce seedlings can be exposed to water stress even under conditions of sufficient soil water and even when they have developed root systems capable of water uptake. During the remainder of the season, the seedlings had Ψ_{min} that never declined below –1.4 MPa, indicating that their root systems had sufficient capability to take up water to meet transpirational demands.

The exposure of seedlings to stress is a normal consequence of the process of lifting, storing, handling, shipping, and planting during forest regeneration. Some degree of stress is unavoidable even under the most ideal planting conditions. Planting stress can be mitigated somewhat by planting seedlings with a high stress resistance (Section 5.1.2.4). Also, planting stress can be minimized by preparing favorable planting sites and planting seedlings properly (Rietveld 1989). Lastly, planting stress can be reduced by timing planting to limit exposure to stressful environmental conditions that reduce both physiological response and root growth of the seedlings (Section 3).

5.4 Establishment phase

Seedlings enter the establishment phase on reforestation sites when they start to develop root systems into the surrounding soil. Therefore, seedlings establish a proper water balance and respond to field site atmospheric conditions without the limitations that can occur when seedlings do not have access to soil water. The establishment phase is a time when seedlings developed as specific stock types or treated with certain nursery cultural practices begin to respond to site conditions. In this section, the performance of container-grown spruce seedlings is examined in relation to short-day nursery cultural effects (as discussed in Section 5.1.1.1), spring and summer planting programs (as discussed in Section 5.1.4.1), and seedling size (as discussed in Section 5.1.4.2). In addition, differences in performance of container-grown and bare-root stock types are discussed. These subsections provide foresters with an appreciation of how various spruce stock types respond to site environmental conditions during the establishment phase.

The establishment phase is also a period when silvicultural practices have reduced the vegetation, thereby creating sites free from competition of established plants (Spies 1997). This occurs because many of the plants found in the understory of the original forest structure have been removed through site preparation or because the original understory has survived the disturbance, but the plants have lost their aboveground parts which may resprout and reoccupy the site at some later date. Before the site is reoccupied with a new vegetation complex, planted spruce seedlings have an opportunity to develop under open site conditions (Fig. 5). As a result, spruce seedlings become exposed to a wider range of environmental conditions (Section 5.2), some of which may be extreme enough to exceed the ability of spruce seedlings to physiologically tolerate environmental stress (defined in Section 3). When this occurs, growth of spruce seedlings on the reforestation site is reduced. On the other hand, this phase can also provide the planted spruce seedlings with ideal environmental conditions that allow for an optimum physiological response and a maximization of their growth potential. An understanding the ecophysiological capability of spruce species in combination with the selection of planting spots that provide desirable microsite environmental conditions can enable foresters to make the proper silvicultural decisions to ensure the planted seedlings respond with rapid plantation establishment.

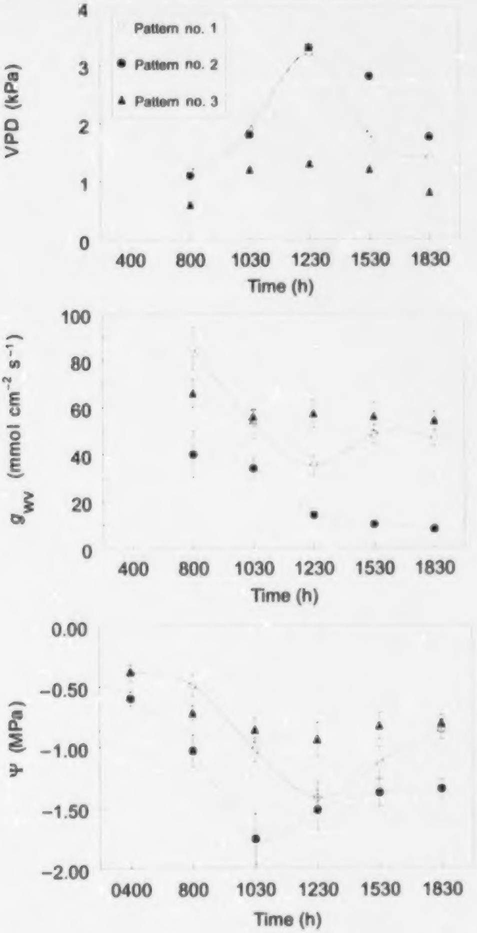
5.4.1 Initial seedling performance

5.4.1.1 Diurnal physiological patterns

Spruce seedlings planted on reforestation sites go through a daily cycle of stomatal opening and closure in relation to changes in the seedling water balance and atmospheric conditions. These interwoven patterns of daily site environmental conditions and physiological responses ultimately affect seedling capability to produce the photosynthates needed for growth. The daily physiological response of spruce seedlings throughout the day is typical of all forest species and generally fits into one of three diurnal patterns (Hinckley et al. 1978), with examples of these patterns described in this section.

In all of the diurnal patterns, g_{wv} is low to negligible in the evening because light is required for stomatal opening (Section 3.1). At night, when stomata are mostly closed, soil water uptake combined with minimal transpiration allows seedlings to rehydrate to a daily maximum Ψ in the predawn hours (Fig. 5.4.1.1) (Section 2.1.2). Light-induced stomatal opening results in increased g_{wv} in the early morning, usually to a daily maximum. It should also be recognized that this early morning period is the time in the day when daytime seedling water status is at a near-optimum level (Section 2.1.2), VPD is low, and PAR is high enough to

Fig. 5.4.1.1. Diurnal patterns of vapor pressure deficit (VPD), needle conductance (g_{wv}), and seedling water potential (Ψ) for spruce seedlings on reforestation sites during the establishment phase. Pattern no. 1 is represented by Engelmann spruce seedlings planted on an afforestation site (Grossnickle 1983). Pattern no. 2 is represented by white spruce seedlings planted on a reforestation site (Grossnickle and Blake 1987*b*). Pattern no. 3 is represented by Engelmann spruce seedlings planted on an afforestation site (Grossnickle and Reid 1984*b*).



allow for maximum P_n to occur (Sections 3.1, 3.2, and 3.5.2.1). Then, one of the following diurnal patterns occur.

In the first diurnal pattern, seedlings are responding to a full range of VPD under nonlimiting soil water. The spruce seedlings have a maximum g_{wv} in the early morning, followed by a decrease in g_{wv} until the middle of the day when VPD has increased to the highest daily level, and seedling Ψ has declined to the daily minimum (Fig. 5.4.1.1). During the afternoon, g_{wv} increases as VPD declines and seedling Ψ increases, although g_{wv} does not increase to the same high values that occur in the early morning hours. In the evening, g_{wv} starts to decline, even at low VPD, as light decreases. On days when this type of diurnal pattern occurs, daytime P_n patterns are directly influenced by daily changes in VPD (Section 3.2) and light (Section 3.1).

In the second diurnal pattern, seedlings are responding to a full range of VPD under moderately limiting soil water. Spruce seedlings have a maximum g_{wv} in the early morning, followed by a decrease in g_{wv} to a low level for the remainder of the day (Fig. 5.4.1.1). Low g_{wv} throughout the day is usually attributed to high VPD and (or) water stress (Section 3.2). Daytime g_{wv} is much lower in these seedlings, in comparison to other diurnal patterns, and this is attributed to the fact that lower g_{wv} is probably due, in part, to the seedlings' limited ability to access soil water during the daylight hours. Daytime closure of the stomata restricts P_n under all daily changes in VPD and light.

In the third diurnal pattern, seedlings are responding to only optimum VPD under nonlimiting soil water. Under these environmental conditions, spruce seedlings have high daily Ψ throughout the day (Fig. 5.4.1.1). Under conditions of low VPD and high seedling Ψ, stomata remain open and P_n remains high if PAR remains high (Sections 3.1, 3.2, and 3.5.2.1). As a result, g_{wv} and P_n remain high throughout the day until light decreases in the evening.

Diurnal changes in seedling water balance, P_n, and g_{wv} are minimal under a number of instances. If seedlings are exposed to low or excessive soil water, stomata do not open and gas exchange processes remain low throughout the day (Sections 3.5.2.1 and 3.5.2.2). In these instances, the lack, or excess, of soil water limits stomatal opening, causing a reduction in P_n. Low soil temperatures also limit the diurnal changes in seedling water balance and gas exchange capacity. Low soil temperatures restrict water uptake, creating seedling water stress and in turn limiting P_n and g_{wv} (Section 3.5.1). In these instances, the ability of the seedling to take up water from the soil system has been reduced, restricting the capability of stomata to open. The diurnal gas exchange pattern is also reduced when seedlings are exposed to summer frosts (Sections 3.3.1 and 5.4.3). These frosts damage the cellular structure of needles, limiting stomatal opening and reducing daily P_n . Thus, deleterious edaphic conditions, or exposure to a growing season frost, can limit spruce seedlings diurnal water balance and gas exchange patterns.

Spruce seedlings, saplings, and older trees typically undergo a daily diurnal Ψ pattern. The range of diurnal Ψ patterns for planted spruce seedlings (Fig. 5.4.1.1) are similar to patterns reported for older spruce trees measured in forests (Lindsay 1971; Wolff et al. 1977; Knapp and Smith 1981). In all of these reported studies, Ψ_{pd} ranged from –0.3 to –0.6 MPa, with daily minimum Ψ between –1.0 and –2.0 MPa during the growing season, depending on edaphic and atmospheric conditions. This indicates that once spruce seedlings have developed an effective root system to absorb soil water, daily diurnal water status is typical of established spruce trees.

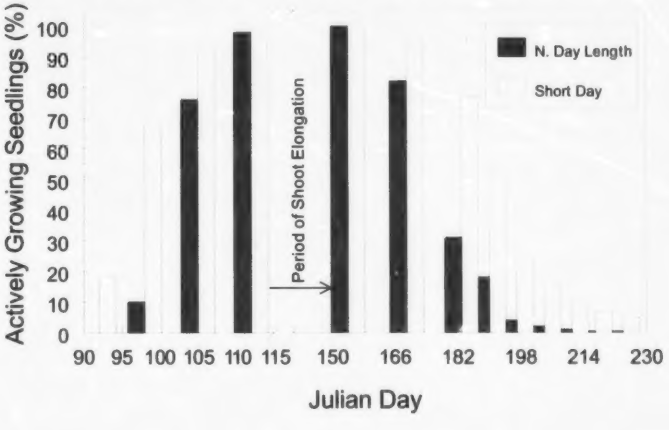
Another phenomenon affecting the diurnal physiological pattern of spruce seedlings during the growing season is the photoperiod length on a northern latitude reforestation site. The length of the photoperiod changes, depending upon the date and latitude of the site (Section 1.1.4). Since stomata open and close in response to light (Section 3.1), daily changes in Ψ depend upon the length of the photoperiod. When the photoperiod is shorter, seedlings recharge with water during the night and reach higher Ψ_{pd}. When darkness is reduced to just a couple of hours (e.g., June 21 at 65° N lat.), spruce trees partially recharge during the twilight period at the end of the day (Wolff et al. 1977) by partial stomatal closure. Extended photoperiods also lengthen the time that spruce trees are exposed to minimum Ψ during the middle of the day (Wolff et al. 1977). As a result, long photoperiods reduce the ability of spruce trees to rehydrate to a daily maximum Ψ during the dark period and to lengthen the time the spruce trees are exposed to minimum Ψ during the day.

5.4.1.2 Short-day nursery culture effects

Short-day nursery cultural treatments are used to stop the growth of rapidly growing containerized seedlings in the nursery and to "harden" the seedlings so they can withstand planting stresses (Section 5.1.1.1). Proper application of the short-day nursery cultural practice improves field performance of spring-planted spruce seedlings.

Short-day treated seedlings used in spring planting programs have a different development pattern than seedlings not treated with a short-day treatment. Short-day treated spruce seedlings show early budbreak of usually around 7 days (Colombo 1986; Silim et al. 1989; Bigras and D'Aoust 1992, 1993; Krasowski et al. 1993*b*; Hawkins et al. 1996) and can have an extended shoot growth phase further into the summer (Krasowski et al. 1993*b*) (Fig. 5.4.1.2). Extension of the growing season by short-day treatments is beneficial because it can result in greater new shoot growth of field-planted spruce seedlings (Odlum and

Fig. 5.4.1.2. The percentage of black spruce seedlings that had budbreak at the beginning of the growing season and budset at the end of the growing season after being treated with either natural day length or short-day treatments in the nursery during the previous growing season (adapted from Odlum and Colombo 1988).



Colombo 1988; Eastham 1991; Hawkins and Draper 1991; Odlum 1991; Hawkins et al. 1996).

A possible negative effect of extending the growing season by short-day treatments is damage of actively growing seedlings by spring or late-summer frost (Sections 1.2.3, 3.7.4, and 5.4.3). Terminal bud damage of short-day treated interior spruce seedlings has been attributed to early growing season frost, although this only occurs on frost-prone sites (Krasowski et al. 1993*b*). This drawback has not prevented short-day treatments from becoming a standard procedure for the production of spring-planted containerized spruce seedlings.

Long-term implications of short-day treatments on plantation performance indicate that the greater shoot growth does not extend beyond the first or second growing season (Story et al. 1995; Hawkins et al. 1996). Thus, the effects of a short-day nursery cultural practice on seedling development disappears after a number of years.

5.4.1.3 Performance of spring- and summer-planted seedlings

Spring- and summer-planted spruce stock types have different growth patterns affecting their morphological development after planting (Section 5.1.4.1). These stock types also have different levels of stress resistance which affect their physiological response to reforestation site environmental conditions (Table 5.1.4.1). Stock type differences can influence seedling performance during establishment and growth phases on reforestation sites.

Spruce seedlings, in general, are planted in the spring from late April through early June or in the summer from late June through early August. Selection of a planting time in either the spring or the summer has a direct bearing on how spruce seedlings initially perform on the reforestation site.

The selection of planting time affects timing of the entire growing season for spring-planted seedlings. After spring planting, spruce seedlings coming out of storage normally require a period of 10–14 days before budbreak occurs (Section 5.1.4.1). The timing of budbreak is dependent upon dormancy status of the seedlings and the thermal input (i.e., warm temperatures) seedlings are exposed to on the field site (Section 2.5). In addition, nursery cultural practices, such as a short-day treatment, can also alter the timing of budbreak (Section 5.4.1.2). After budbreak occurs, spruce species grow for a period of between 8 and 12 weeks, with rapid shoot growth occurring over a 4-week period in the middle of this shoot elongation phase (Section 2.6.1.1). The actual cessation of this shoot growth period is triggered by a reduced photoperiod length and decreasing site temperatures. Thereafter, bud induction and complete development of needle primordia in the bud can take up to another 6–10 weeks (Section 2.6.1.1). Spring-planted spruce seedlings require from approximately 16 to 22 weeks to complete the process of shoot development. Timing of planting in the spring can determine whether spruce seedlings have a sufficient length of time to undergo all normal shoot development processes before late-summer photoperiods and site temperatures limit this development.

For summer planting, spruce seedlings undergo rapid changes in stress resistance and root growth capability, rather than shoot development, across the planting window. These changes are part of the natural seasonal phenological cycle inherent in spruce species (Section 3.9). Spruce seedlings planted early in the summer planting period typically have a high level of performance (i.e., high P_n capability and high root growth capacity), although a low stress resistance (i.e., drought and freezing tolerance) (Section 5.1.4.1). After budset, these parameters can change quite rapidly over the 4–6-week summer planting window (Sections 5.1.1.1 and 5.1.4.1). These changes can alter the capability of spruce seedlings to properly respond to site environmental conditions.

In the year seedlings are planted on a reforestation site, spring- and summer-planted seedlings have different patterns of morphological development. Spring-planted spruce seedlings have new shoot development, while summer-planted seedlings have no new shoot development (Table 5.4.1.3). Due to this first-year shoot growth, seedlings planted in the spring can have double the number of branches and buds (upwards of 100 buds along their shoots) and a larger crown width than summer-planted seedlings. As a result, spring-planted seedlings have a larger overall shoot system than summer-planted seedlings at the end of the first growing season. This indicates that when both stock types are ready to break bud the following spring, seedlings planted the previous spring have approximately twice the number of locations for shoot growth to occur.

Table 5.4.1.3. Stock type morphological characterization of interior spruce seedlings ($N = 20$: mean ± SE) used in spring (FS–1+0) and summer (SP–2+0) planting programs over two growing seasons on a boreal reforestation site (Prince George, B.C., 54° N lat.) (Grossnickle and Folk, unreported data).

	Year 1		Year 2	
Stock type[a]	FS–1+0	SP–2+0	FS–1+0	SP–2+0
New shoot growth (cm)	10.1 ± 1.4	None	5.2 ± 0.2	14.3 ± 1.1
Total shoot height (cm)	29.4 ± 0.8	22.8 ± 0.5	34.3 ± 0.3	34.2 ± 0.6
Diameter (mm)	5.7 ± 0.3	4.2 ± 0.1	8.3 ± 0.3	7.3 ± 0.2
Height to diameter ratio (cm/mm)	4.2 ± 0.3	5.6 ± 0.3	4.1 ± 0.1	4.8 ± 0.2
Number of branches	21 ± 2	10 ± 1	39 ± 4	23 ± 2
Number of buds	98 ± 7	51 ± 3	164 ± 17	126 ± 12
Terminal bud needle primordia	124 ± 18	251 ± 24	—	—
Crown width (cm)	15.4 ± 1.3	11.9 ± 0.4	17.8 ± 0.9	15.6 ± 0.9
Root development into the soil (g DW)	0.6 ± 0.1	0.5 ± 0.1	—	—
Shoot to root ratio (g/g)	1.4 ± 0.2	1.6 ± 0.1	—	—

[a] FS–1+0, frozen-stored 1+0 seedlings planted in early June; SP–2+0, hot-lifted 2+0 seedlings planted in early July.

Both stock types have comparable height to diameter ratios, root development, and shoot to root ratios after the first growing season, indicating a similar level of overall morphological balance.

Summer-planted seedlings have budset and the initial stages of needle primordia development in the nursery before being shipped to the field. As a result, these seedlings have twice the number of needle primordia in their terminal buds at the end of the growing season when compared to spring-planted seedlings (Table 5.4.1.3). This indicates that summer-planted seedlings have a predetermined shoot growth potential for the next growing season that is twice that of the spring-planted seedlings. If summer-planted seedlings do not have greater predetermined shoot growth potential, this stock type has no strategic advantage over spring-planted seedlings. This was evident in a study on black spruce where the first-year growth advantage of spring-planted seedlings was never made up by summer-planted seedlings even though relative height growth rates were similar over the following growing seasons (Fleming and Wood 1996). It is imperative that nursery cultural practices confer an adequate predetermined shoot growth potential in summer-planted seedlings if this stock type is going to have good establishment on the reforestation site.

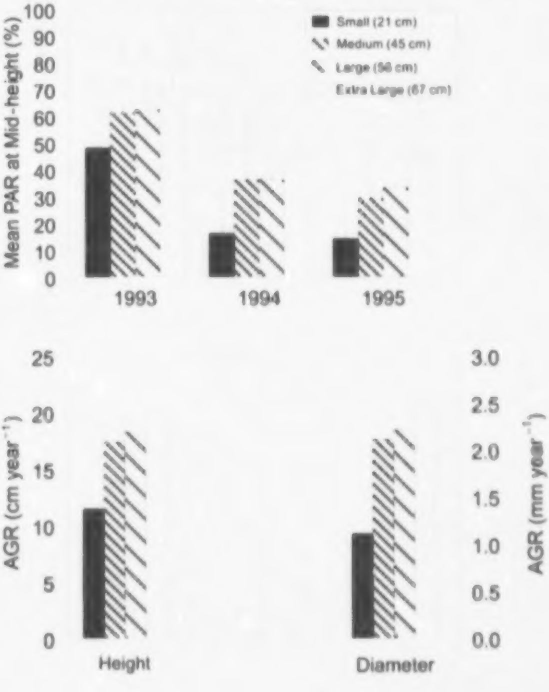
During the second growing season, spring- and summer-planted seedlings also have different patterns of morphological development. Summer-planted seedlings have double the rate of new shoot growth as seedlings planted in the spring, which results in both stock types having comparable shoot height and crown width after two field seasons (Table 5.4.1.3). Seedlings planted in the spring still have a slightly larger diameter and thus have a lower height to diameter ratio. Spring-planted seedlings also have a greater number of branches and buds, indicating a greater number of locations for shoot growth to occur in the coming spring. Morphological development over two growing seasons shows the differences between the spring- and summer-planted stock types becoming less noticeable. This indicates that as seedlings grow and become established on the reforestation site, the influence of the original stock type characteristics diminishes.

5.4.1.4 Performance related to initial seedling size

Spruce seedlings grown in large-volume container cavities have greater shoot and root sizes, which allow the seedling to occupy a greater area within the planting spot (Section 5.1.4.2). These larger seedlings also have a greater number of locations for shoot growth (i.e., greater number of branches and buds), which increases the potential to occupy a greater area within the planting spot. However, a morphologically larger seedling does not have additional physiological performance and material stock quality attributes that enhance performance under optimum or limiting environmental conditions (Section 5.1.4.2). A benefit of a larger seedling in relation to its physiological performance is the potential for greater seedling photosynthetic capacity. This ensures faster growth, thus the potential for rapid site occupation and access of site resources during the establishment phase. It is this greater size of the root and shoot systems that confers any additional benefit to larger seedlings during establishment on the reforestation site. However, foresters must recognize that large planting stock can provide both benefits as well as risks to the establishment of a forest plantation.

Planting larger seedlings can be beneficial to seedling establishment. A number of studies have found that planting larger, compared to smaller, conifer seedlings on sites with vegetation competition resulted in better growth up to 8 years after planting (Balneaves 1989; Newton et al. 1993; South et al. 1993; South et al. 1995; Zwolinski et al. 1996). This pattern was also evident in field trials with Sitka (South and Mason 1993), white (McMinn 1982*b*), and black spruces (Jobidon et al. 1998). In the study on black spruce (Jobidon et al. 1998), larger stock had a greater exposure to the growing season PAR available to shoot systems over a 3-year period, which resulted in greater shoot growth (Fig. 5.4.1.4). Spruce species have a rapid increase in P_n as PAR increases to approximately 25% full sunlight, with a continued gradual increase in P_n at further increases in light, and this has a direct effect on shoot growth (Section 3.1). Competition for light between planted seedlings and competing vegetation is one of the main limiting environmental factors that affect the performance of seedlings in the transitional phase of plantation development (Section 5.5.1). The use of larger

Fig. 5.4.1.4. The mean percentage of photosynthetically active radiation (PAR) transmitted at the mid-height of black spruce seedlings of four initial sizes, and mean absolute growth rate (AGR) for height and diameter over the 3-year period on a reforestation site in southern Quebec (adapted from Jobidon et al. 1998).



seedlings may be a good silvicultural strategy if vegetation competition is a major factor limiting plantation establishment.

Larger container-grown stock size does not confer an advantage over the surrounding competition unless the size difference is large enough to dramatically improve field performance. Paterson (1997) planted black spruce container-grown stock with a modest range in size (i.e., 23.1–19.6 cm in height and 2.7–2.0 mm in diameter) and found that, after 5 years, survival and current annual height increment were comparable, although originally larger stock was still bigger. These findings indicate that larger container-grown stock needs to be originally large enough to capture more of the site resources from the competition in order to justify its use in a reforestation program.

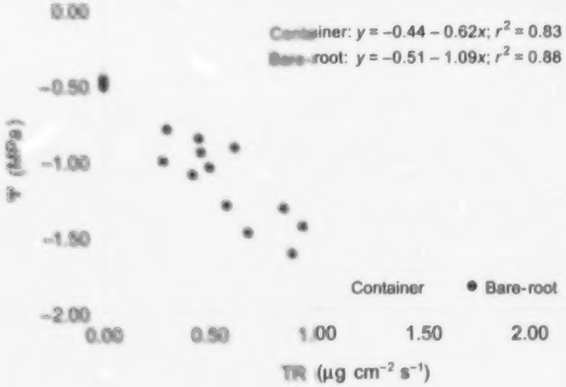
Planting seedlings of larger size can also create risks in establishing a plantation. This may occur where limiting environmental conditions can put seedlings with a large shoot to root balance under physiological stress. Under dry soil conditions, larger conifer seedlings had greater water stress (Rose et al. 1993; Stewart and Bernier 1995) or reduced growth (Baer et al. 1977; Hahn and Smith 1983) than smaller seedlings. Under dry conditions, black spruce seedlings with very large shoot systems (i.e., six times the foliar mass of small seedlings) had greater water stress and reduced P_n compared to seedlings with smaller shoot systems (Lamhamedi et al. 1997). As the seedling shoot system reaches a certain size, the increased foliar mass can increase the seedling's susceptibility to water stress. This can be a problem in newly planted seedlings that have restricted root development. The susceptibility of larger seedlings to be exposed to water stress at planting is mitigated if seedlings have the capability to quickly develop new roots. Large container-grown Engelmann spruce seedlings had increased first-year survival compared to smaller seedlings (Hines and Long 1986). Hines and Long (1986) found that increased survival in larger seedlings was related to greater root growth over the initial 4-week period after planting, which reduced seedling water stress (i.e., Section 5.3: Planting stress). In most instances, spruce seedlings show a general trend of greater new root growth with a greater original root system size (Section 5.1.2.2), which allows larger spruce seedlings to generate enough roots to reduce the shoot to root balance and avoid planting stress conditions. However, increased root growth does not always occur in larger seedlings having bigger root systems (e.g., Fig. 5.1.2.2*b* and Table 5.1.4.2), and this variability can be related to stock type, nursery cultural practices, and genetic source. In addition, restricted root development of newly planted seedlings can be limited by field site edaphic conditions (Section 3.5). Caution should be used when considering whether to plant large stock on sites that can limit initial seedling establishment.

5.4.1.5 Container-grown versus bare-root seedling performance

Trials with container-grown and bare-root seedlings demonstrated that any detectable differences between these stock types in survival occurred primarily during the first year or two of establishment on the reforestation site. For the most part, containerized spruce seedlings had greater initial survival than bare-root seedlings (Gardner 1982; Scarratt 1982; Vyse 1982; Alm 1983; Burdett et al. 1984; Wood 1984; LePage and Pollack 1986; Scarratt and Wood 1988; Nilsson and Örlander 1995), although work with Sitka spruce found greater survival in bare-root compared to container-grown seedlings (Mason and Biggin 1988). After the initial establishment period, further seedling mortality was minimal in both stock types, and most differences evident in the first growing season were maintained for up to 10 (Wood 1990) to 14 (LePage and Pollack 1986) years.

Reduced survival of bare-root, compared to container-grown, seedlings is possibly related to greater planting stress (Section 5.3). One reason this occurs is that bare-root seedlings can have greater resistance to water flow through the SPAC, compared to container-grown seedlings, just after being planted on a reforestation site (Fig. 5.4.1.5). This initially higher resistance to water flow through the SPAC occurs in bare-root seedlings due to the initial suberized nature of their root systems, resulting in reduced root system permeability (Section 2.1.2). Low root system permeability is a phenomenon that has been reported in bare-root white spruce and black spruce seedlings (Grossnickle and Blake 1985; Grossnickle 1987, 1988*a*). Newly planted bare-root seedlings also have root confinement and (or) poor root–soil contact, factors that also influence planting stress in newly planted container-grown seedlings. These stock type differences in water uptake capability may explain why recently planted bare-root Norway spruce seedlings had greater mortality on a reforestation site, which was attributed to water stress, than container-grown seedlings during a dry growing season (Nilsson and Örlander 1995). If bare-root seedlings are able to regenerate new roots, root system permeability increases and water stress is reduced (Grossnickle and Blake 1985; Grossnickle 1987, 1988*a*), allowing seedlings to resume normal physiological processes related to growth.

Fig. 5.4.1.5. The relationship between transpiration rate (TR) and shoot water potential (Ψ) for recently planted bare-root (1.5+1.5) and container-grown (1+0) black spruce seedlings over the first 5 weeks after planting on a reforestation site (adapted from Grossnickle and Blake 1987*b*).



In most of the early trials comparing bare-root versus container-grown stock types, bare-root seedlings have been larger at planting (Gardner 1982; McClain 1982; Vyse 1982; Wood 1984; Burdett et al. 1984; Wood and Dominy 1985; LePage and Pollack 1986; Scarratt and Wood 1988; Sutherland and Newsome 1988). It was felt that container-grown seedlings had to have superior growth during the plantation establishment stage to minimize the long-term effect of their initially smaller size. Some of these earlier studies found container-grown seedlings had greater incremental growth just after planting on a reforestation site (Scarratt 1982; Vyse 1982; Burdett et al. 1984; Scarratt and Wood 1988; Wood and Dominy 1985; LePage and Pollack 1986; Wood 1990).

Greater initial growth for container-grown seedlings could be due to a number of factors. First, in a number of instances, container-grown seedlings are reported to have greater root growth than bare-root seedlings under controlled root growth capacity testing (Binder et al. 1990) and during the first growing season on a reforestation site (Burdett et al. 1984; Grossnickle and Blake 1987*b*). Burdett and co-workers (1984) felt that this improved root growth minimized water stress and thus relieved the planting stress phenomenon in container-grown, compared to bare-root, seedlings and allowed these seedlings greater access to soil nutrients. Second, containerized seedlings are grown within a favorable greenhouse environment, which allows this stock type to develop a larger complement of needle primordia within buds (Section 2.6.1.1). Thus, container-grown seedlings can have a greater predetermined shoot growth potential than bare-root seedlings over the first growing season. If smaller container-grown stock is to match or improve on the performance of originally larger bare-root stock, then increased growth needs to be achieved in the first few years after planting (Scarratt 1982). Thereafter, relative height differences between the two stock types diminish over time (Vyse 1982; Burdett et al. 1984; LePage and Pollack 1986; Wood 1990).

Studies have also reported that the initial difference between stock types (i.e., greater size of bare-root stock type) was maintained during plantation development (Gardner 1982; McClain 1982; Wood and Dominy 1985; LePage and Pollack 1986; Mason and Biggin 1988; Sutherland and Newsome 1988; Wood 1990; Cole et al. 1999; Nilsson and Örlander 1999). On sites with heavy competition, initially larger bare-root black spruce seedlings had volume growth rates that were between 18 and 22% greater than smaller container-grown seedlings, although on weeded sites the larger bare-root seedlings only grew at a 4–7% greater growth rate (Fleming and Wood 1996). Bare-root seedlings are not exposed to planting stress when they are planted on reforestation sites with adequate soil water (Section 5.3). Thus, initially larger seedling size can provide a greater potential for seedling establishment and growth on reforestation sites where competition is a factor (Section 5.4.1.4). In certain instances, the use of larger bare-root spruce seedlings can confer a distinct advantage over smaller container-grown seedlings. This is especially evident on mesic reforestation sites where competition is prevalent.

One way to overcome the initial smaller size of containerized seedlings is to grow larger seedlings in containers. For example, in British Columbia, 1.5+1.5 bare-root interior spruce seedlings have a target height of 25 cm and target diameter of 4.5 mm, while medium and large 2+0 bare-root interior spruce seedlings have target heights of 27 and 40 cm, and target diameters of 5.0 and 6.5 mm, respectively (Scagel et al. 1993). These shoot sizes are comparable to larger container-grown interior spruce stock types currently being produced (Section 5.1.4.2). In another example, Ontario bare-root spruce seedlings have median target heights of 20, 32.5, and 50 cm and target diameters of 3.0+, 4.0+, and 6.0+ mm for medium, large, and extra large stock types, respectively (Johnson et al. 1996). In comparison, container-grown spruce seedlings in Ontario have median targets of 20 and 32.5 cm and target diameters of 2.0 and 2.8 mm for medium and large stock types, respectively (Johnson et al. 1996). Thus, results reported in earlier studies on shoot development differences between container-grown and bare-root seedlings in forest plantations may not be as much of a concern, based on large container-grown stock types currently being produced by the conifer nursery industry in Canada. Further work is required to assess the performance of currently produced bare-root and container-grown seedlings to develop up-to-date stock type recommendation standards.

5.4.2 Frost heaving

Frost heaving occurs on regeneration sites that have fine-textured soils with a high amount of soil water and exposure to below-freezing air temperatures (Section 1.2.5). When site air temperatures are just below freezing, temperatures in the upper soil layer fluctuate around 0°C, resulting in the formation of ice lenses. These ice lenses cause seedlings to frost heave. Newly planted seedlings are susceptible to the process of frost heaving due to lack of adequate root system development needed to anchor the seedlings into the soil (Örlander et al. 1990; Goulet 1995).

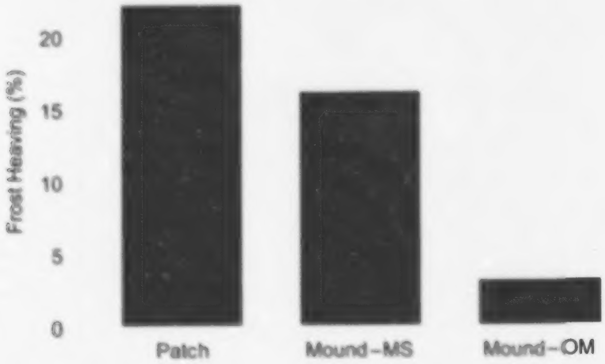
The primary effects of frost heaving on the physiological performance of newly planted seedlings fit into two categories (Goulet 1995). First, frost heaving lifts the seedling root system out into the air and exposes roots to desiccation. Second, frost heaving causes the breakage of newly developed roots and reduces effective root–soil contact. Frost heaving creates conditions that disrupt water flow through the SPAC pathway by reduction of root system size and distribution, and disruption of root–soil contact, thereby causing planting stress (i.e., water stress) to be prolonged (Section 5.3). Long-term effects of frost heaving include reduced seedling establishment and growth on reforestation sites.

Field performance of frost-heaved spruce seedlings is restricted because of planting stress. Spruce seedlings planted in exposed mineral soils on sites prone to summer frost have reduced survival, with frost heaving a primary cause of increased mortality (Nobel and Alexander 1977; Shaw et al. 1987). In a number of instances, reduction in shoot development of spruce seedlings was directly attributed to frost heaving (MacGillivray and Hartley 1973; Söderstöm 1973; Low

1975; Zalasky 1980). The loss of growth in some white spruce plantations was attributed to an annual natural pruning of roots through frost heaving, leaving root systems either deformed or partially exposed (Sutton 1992). Root deformity in young spruce seedlings due to frost heaving has long-term implications on plantation performance because it reduces stability, thus increasing potential blow-down within the plantation (Shaw et al. 1987; Sutton 1992).

Frost heaving can be exacerbated or mitigated by silvicultural regeneration practices. On some sites, removal of overstory vegetation can create conditions conducive to frost heaving (Graber 1971). Sutton (1970) found that white spruce seedlings that appeared to be well established, when released from weeds, were heaved from the soil through frost action. Also, site preparation treatments that removed the organic surface layer from fine-textured soils increased the incidence of frost heaving (Fig. 5.4.2). Frost heaving can be controlled by retention of some overstory cover, mulching of exposed mineral planting spots, or through site preparation techniques that create microsites having an overlying organic layer (e.g., inverted humus mounds). In addition, deep planting of large stock is recommended under certain conditions (i.e., where high water tables and (or) low soil temperatures do not occur) to ensure adequate root development, keeping seedlings firmly anchored into the soil (Örlander et al. 1990; Goulet 1995).

Fig. 5.4.2. Frost heaving frequency of container-grown conifer seedlings planted on a sandy-silt moraine under various site preparation treatments in northern Sweden (adapted from Örlander et al. 1990). Mounds were located on mineral soil (MS) or organic matter (OM).



5.4.3 Summer frost and late-winter desiccation

Summer frosts occur due to radiative heat loss from the ground surface under clear night sky weather conditions or to the movement of cold air downslope through the advection process (Section 1.2.3). These frosts primarily occur at the beginning and end of the growing season, although frost can occur at any time of the year on clear-cut reforestation sites within the boreal forest. On sites where cover vegetation has been removed, air temperatures near the soil surface (at 5–10 cm) can be 2–6°C lower than air temperatures found under a vegetation canopy (Stathers 1989; Örlander et al. 1990; Groot and Carlson 1996; Groot et al. 1997), causing a greater number of frosts to occur during the growing season on a reforestation, compared to forested, site.

Freezing temperatures during the summer months coincide with the period in which spruce seedlings are at their lowest level of freezing tolerance (Section 3.7.4). Any exposure to freezing temperatures causes a reduction in physiological performance and morphological development (Section 3.3.1). Most of the frost damage in field-planted spruce seedlings seems to be confined to the buds, newly flushed needles, and succulent shoots of spruce seedlings (Clements et al. 1972; Stiell 1976; Örlander et al. 1990; LePage and Coates 1994), and these are the shoot structures that have the lowest level of freezing tolerance during the growing season (Section 3.7.4).

The time at which spruce seedlings are exposed to frost during the growing season affects subsequent morphological development (Grossnickle, personal observation). Bud development is arrested when frost damages the bud during the initial stages of bud activity, prior to budbreak, in the spring. Damaged buds look viable, yet do not break bud. When a severe enough frost occurs as shoots are emerging, shoot systems can be damaged. Damaged shoots turn brown and fall off the seedling, leaving no visible damage to the shoot system. When a lethal frost occurs after the shoot system has elongated, the needles turn brown and fall off, leaving the dead stem. After any of these frosts, no new shoot growth occurs from the damaged shoot in that growing season.

During the growing season that follows a damaging frost, shoot growth of spruce seedlings occurs from lateral buds just below the damaged region of the shoot system (Grossnickle, personal observation). If the terminal shoot is damaged, a number of the lateral shoots can grow upwards, resulting in a forked top. Usually, although not always, one of these new terminal shoots becomes dominant after a number of years. Lateral branches can develop a "bushy" structural appearance due to the loss of a terminal bud or shoot to a frost. This creates a seedling with a compact shoot structure that has many lateral branches within the crown. Frosts that damage shoots have a marked effect on subsequent growth patterns of seedlings. This damage is manifested although a reduction in shoot growth as well as an alteration of the shoot form. This reduction in subsequent shoot development due to a severe summer frost can reduce the capability of spruce seedlings to become established on reforestation sites.

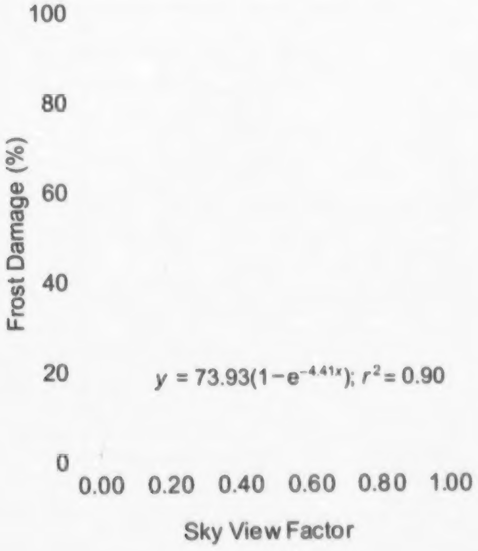
Frosts during the growing season are considered the chief problem in establishing tree plantations in northern latitude forests (Sakai and Larcher 1987). In addition, the number of frosts tends to increase with decreasing levels of competing vegetation. There is a greater occurrence of frosts causing damage to young plantations of spruce seedlings on open sites compared to forested sites (Clements et al. 1972; Harding 1986; Christersson and von Fricks 1988; Sutton

1992; Groot and Carlson 1996; Tanner et al. 1996). The percentage of white spruce seedlings with moderate or severe damage as a result of spring frosts increases dramatically at >20% exposure to the sky (Fig. 5.4.3*a*). Geiger (1980) reported that there is a direct relationship between the size of a forest clearing (i.e., up to 3 ha in size) and the lowest night temperatures, which increases the chances of a frost occurring during the springtime. On a frost-prone site, 71% of interior spruce seedlings had frost damage at the end of the first growing season where vegetation cover was <15% (LePage and Coates 1994). Further development of interior spruce height growth over a 5-year period was reduced due to frost damage, where vegetation cover ranged from 8 to 17%. Alternative silvicultural systems that retain a partial forest canopy reduce the frequency of frosts; this is discussed later in this treatise (Section 5.6).

On sites subjected to frequent summer frosts, reductions in cover may be more detrimental than beneficial to the initial performance of spruce seedlings. White spruce seedlings under a vegetation canopy had higher seasonal P_n in the spring and fall than open-grown seedlings, and this was attributed to reduced exposure to freezing temperatures for seedlings covered by vegetation (Man and Lieffers 1997). Ball (1994) suggests that the optimum regeneration niche on open field sites are microsites that protect seedlings from both radiative frosts and intense sunlight, as this combination of environmental conditions is known to cause damage to the photosynthetic system in spruce seedlings (Section 3.3.1).

In the long-term, interior spruce height growth was greatest on sites where vegetation was <8%, indicating that seedlings can ultimately outgrow the potential

Fig. 5.4.3*a*. Incidence of medium to heavy summer frost damage to white spruce seedlings versus the sky view factor of the opening (adapted from Groot and Carlson 1996).

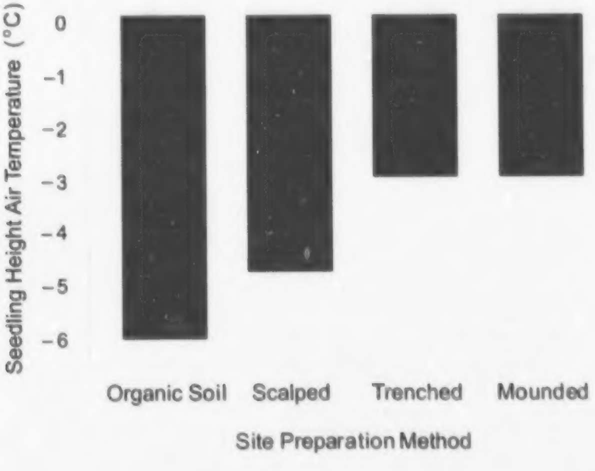


for frost damage, given reduced competition for site resources (LePage and Coates 1994). Thus, spruce seedlings can reach a shoot size that is not influenced by the site microclimate near the soil surface where frosts are prone to occur.

On sites with no vegetation cover, site preparation treatments can sometimes reduce the number of frosts that occur during the growing season. Treatments such as burning, scalping, trenching, and mounding can decrease the risk of radiation frost damage to conifer seedlings (Stathers 1989; Steen et al. 1990; Örlander et al. 1990) (Fig. 5.4.3*b*). These treatments allow for the mixing of warm overlying air and for airflow to occur near the soil surface, thereby increasing air temperature by just a few degrees (Stathers 1989). Removal of grass and surface organic layers can also decrease the risk of radiation frosts. In cold, wet areas, mineral mounds that raise the seedling out of the cold air layer can be effective in reducing the risk of radiation frosts (Steen et al. 1990). Planting seedlings near large stumps or fallen logs may also provide additional heat through the reradiation of stored energy during the night (Spittlehouse and Stathers 1990). This microsite effect can cause enough of an increase to bring temperatures above the critical freezing mark and prevent damage to actively growing seedlings during the growing season.

There have been reports of extensive damage to spruce seedling plantations during the first postplanting winter (Herring and Letchford 1987; Krasowski et al. 1993*a*, 1995). This damage has been attributed to freeze desiccation. When the snowpack melts during the late winter and early spring, shoots can be exposed to above-freezing daytime air temperatures, plus increased light and VPD during the late winter and early spring (Krasowski et al. 1995). Shoot systems exposed above the snowpack undergo water stress that can become lethal if

Fig. 5.4.3*b*. The lowest air temperature at seedling height in different site preparation treatments during a nighttime summer frost on a northern latitude reforestation site (adapted from Stathers 1989).



the frozen soils limit water uptake required to meet the low transpiration levels of partially open stomata and (or) cuticular transpiration occurring as shoots are exposed to late-winter and springtime evaporative demand of the air (Section 3.7.5). It is unclear whether this is a persistent problem for seedlings on sites that have the potential for low snowpack or whether 3–4 years of deep snowpack are required to allow seedlings to grow to a size that reduces the risk of overwinter shoot damage due to winter desiccation.

Freeze desiccation is believed to be exacerbated by the root development patterns of recently planted container-grown spruce seedlings (Krasowski et al. 1996). Spruce seedlings grown in containers initially have roots that develop primarily out of the bottom rather than the top portion of the container plug (Section 2.6.2.2). During the late winter and early spring, the soil in the boreal forest is typically frozen to a depth beyond 5 cm, with soil temperatures consistently below 5°C until early May (Stathers and Spittlehouse 1990; Krasowski et al. 1995) (Section 1.2.1). Since the majority of water-absorbing roots of recently planted container-grown seedlings are in the frozen portion of the soil profile (i.e., from 5 to 15 cm in depth), Krasowski et al. (1996) theorized that seedlings cannot absorb enough water to meet the transpirational demand placed upon their shoot systems. The ability of spruce seedlings to take up water from the soil decreases dramatically as soil temperatures decline to freezing, with water uptake through the roots being nonexistent in frozen soil (Section 3.5.1), which can result in increased seedling water stress (Section 3.7.5). Krasowski et al. (1996) noted that naturally established and older container-grown seedlings did not visibly suffer from desiccation injury and had more extensive root systems throughout the soil profile; this may have helped these seedlings to avoid late-winter and early-spring desiccation. A lower incidence of desiccation injury occurred in seedlings planted on plowed sites or on planting mounds (Krasowski 1996), and these microsites may have afforded deeper daytime thawing of the soil profile during the late winter and early spring, enabling spruce seedlings to take up sufficient soil water to prevent desiccation injury.

5.4.4 High soil surface temperatures

High soil surface temperatures can occur on open reforestation sites within the northern latitude forest as the result of site and atmospheric factors. First, soil surfaces with high organic matter content and dark coloration have a higher capacity for heat build-up (Section 1.2.4). In certain instances, soil surface temperatures can exceed 50°C on open reforestation sites throughout the northern latitude forest region. Second, clear sunny days and a lack of wind to dissipate heat build-up along the soil surface create atmospheric conditions causing an increase in air temperature (Section 1.4), which leads to high VPD (Section 1.3.2) at seedling shoot height. An increase in soil surface temperatures typically increases the VPD of the air just above the soil surface (Ripley and Redmann

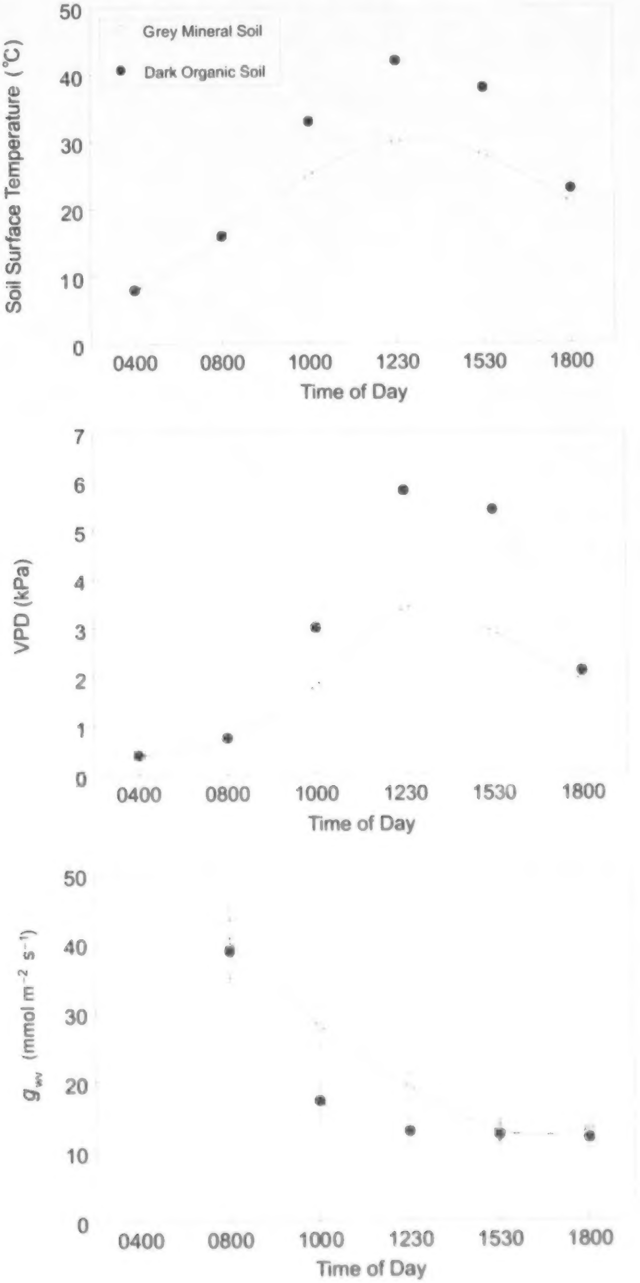
1976). This is why sites that can have high soil surface temperatures provide a poor microenvironment for seed germination and seedling establishment (Smith 1951; Vaartaja 1954; Hungerford and Babbitt 1987).

Conifer seedling shoots can be damaged when soil surface temperatures exceed 50°C on reforestation sites (Maguire 1955; Helgerson 1990). Seedlings express heat damage through formation of lesions or abnormal swelling of the stem near the soil surface (Helgerson 1990). In a study of western conifers, Engelmann spruce was determined to have the lowest level of tolerance to high temperatures (Seidel 1986). Actively growing spruce seedlings have shoot damage at temperatures that exceed 45°C, with the level of damage increasing due to either the length of exposure or to exposure to higher temperature conditions (Section 3.3.2). White (MacHattie and Horton 1963) and Engelmann (Nobel and Alexander 1977) spruce mortality on reforestation sites has been attributed to high temperatures.

In many instances, high but nonlethal soil surface temperatures during the summer alter the diurnal physiological processes of planted spruce seedlings. For example, on clear sunny days with no wind along the soil surface, surface temperatures of dark-colored soils reached up to ~40°C, resulting in increased midday VPD (Fig. 5.4.4). Engelmann spruce seedlings grown in this dark organic matter were exposed to 18% higher needle temperatures (~3–5°C) and 33% greater VPD during the early afternoon, when compared to seedlings growing in grey mineral soil. These atmospheric conditions caused a reduction in g_{wv} for Engelmann spruce seedlings growing in the dark organic matter compared to mineral soil. This reduction in g_{wv} occurred even though all seedlings had similar Ψ_{pd} (i.e., –0.45 and –0.40 MPa for seedlings growing in the dark organic matter and mineral soil, respectively). A reduction of g_{wv} under higher VPD is a typical response for spruce seedlings (Section 3.2).

The application of silvicultural practices to alter the structure or constituency of the soil surface, or reduce the amount of incoming solar radiation received at the soil surface, mitigates the potential of heat damage to recently planted spruce seedlings (Helgerson 1990). Practices such as removing surface litter or organic matter from the base of seedlings reduce heat load to the seedling stem. Planting seedlings on the north-facing side of trenches or furrows created through mechanical site preparation treatments also reduce heat loads. Shade from natural site features such as rocks, stumps, and coarse woody debris can also reduce soil surface temperatures. Shading through artificial means (e.g., shade cards) or by leaving an adequate overstory vegetation cover can also reduce the risk of seedling exposure to high soil surface temperatures. These same silvicultural practices can create microsites having low soil temperatures, which are also known to limit spruce seedling performance on northern latitude reforestation sites (Section 3.5.1). Before applying these types of silvicultural practices to recently planted spruce seedlings, foresters need to identify whether a high soil surface temperature is likely to be a site environmental factor limiting spruce seedling performance.

Fig. 5.4.4. Diurnal pattern of soil surface temperature, vapor pressure deficit (VPD) measured at seedling height, and needle conductance (g_{wv}) for Engelmann spruce seedlings on a clear sunny summer day for microsites having either a grey mineral soil or dark organic matter soil surface layer (adapted from Grossnickle and Reid 1984*b*).



5.4.5 Flooding

Flooded soils can occur on northern latitude reforestation sites located in low-lying peatlands or bogs, poorly drained alluvial valley bottoms, and floodplains of river valleys. Flooding causes forest soils to become anaerobic (Section 1.3.1) and have low thermal diffusivity (Section 1.2.4), which keeps soils cold throughout the growing season. These soil conditions lead to reduced physiological activity (i.e., gas exchange and nutrient uptake) and growth of spruce seedlings (Sections 3.5.2.2 and 3.6.1). If flooded conditions are severe, planted seedlings undergo stress and possibly die (Section 3.5.2.2). Silvicultural practices that raise the elevation of the planting spots, modify the aboveground microclimate, or increase the drainage of water from the site have led to improved seedling establishment on sites prone to flooding.

Site preparation treatments that raise the planting spots above the water table have been effective in improving spruce seedling establishment. Raised planting spots provide sites of increased soil aeration for seedlings planted in soils where there is a high water table (Macadam 1988; McMinn and Hedin 1990; Sutton 1993; Yole and Kranabetter 1996*a*) (Fig. 5.4.5*a*). The raised planting spots also increase soil temperatures throughout the growing season (Macadam 1988). These raised planting spots provide a location for boreal conifer seedlings to develop roots into the soil (Söderstöm 1981; von der Gönna 1989) so they can become established and have enhanced shoot growth (Söderstöm 1981; Schaible and Dickson 1990; Hånell 1992). For example, black spruce seedlings planted on raised planting spots had greater shoot growth over two growing seasons (Fig. 5.4.5*b*). This improved growth was attributed to better aerated soils and warmer rooting zone temperatures in the raised planting spots, which allowed for improved nutrient uptake, resulting in an increase in both needle N and Ca concentrations (Roy et al. 1999). The long-term growth (i.e., over 8 years) of interior spruce seedlings can be improved by up to 40% by using raised planting spots on sites with seasonally wet soils (Macadam and Bedford 1998). Raised

Fig. 5.4.5*a*. Soil water potential (Ψ_{soil}) at 10 cm throughout the growing season for different site preparation treatments in hygric soils on a boreal reforestation site in north-central British Columbia (adapted from Macadam 1988).

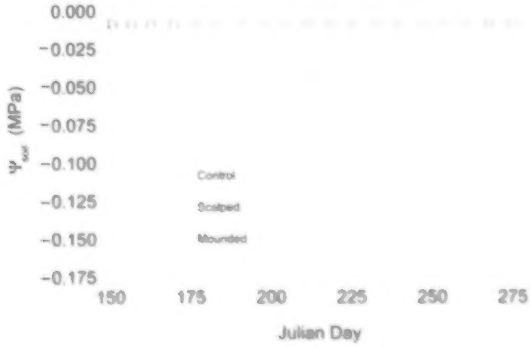
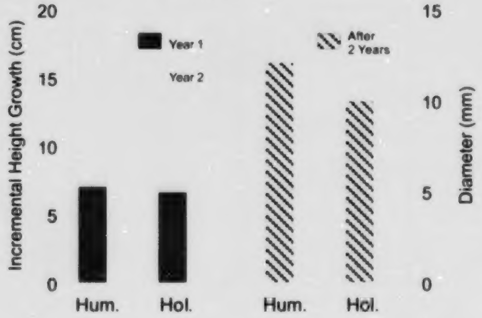


Fig. 5.4.5*b*. Height growth and diameter of black spruce seedlings on hummock and hollow planting spots over two growing seasons in a wetlands boreal reforestation site (Forêt de Beaurivage, Que., 46° N lat.) (adapted from Roy et al. 1999). Average depths of the aerobic layers were 26.2 and 15.1 cm on hummocks and hollows, respectively, over the two growing seasons.



planting spots also provide a microtopographic position that increases the survival of seedlings in flooded soils (Macadam and Bedford 1998; Roy et al. 1999), although if the water table drops during the growing season, these raised spots can cause seedling water stress and higher mortality (Rothwell et al. 1993).

Site preparation treatments that remove vegetation and slash from the soil surface (i.e., windrowing or broadcast burning) can increase the radiation reaching the soil surface, thereby increasing evaporation from the soil surface and causing a moderate reduction of soil water in saturated soils (Yole and Kranabetter 1996*a*). Aerated soils also have a higher thermal diffusivity that allows greater heat penetration downward into a moist, compared to saturated, soil profile (Section 1.2.4). Opening up low-lying reforestation sites can also increase air temperatures at the soil surface and improve the soil temperatures within the effective rooting zone of recently planted seedlings.

Site preparation treatments that remove water from poorly drained reforestation sites also improve the growth of planted spruce seedlings. In this silvicultural practice, ditches are cut (i.e., 0.5–1.0 m in depth) across the contours of a site to increase drainage, thereby lowering the water table and increasing soil temperatures (Lieffers and Rothwell 1987) and nutrient availability (Lieffers and MacDonald 1990; MacDonald and Lieffers 1990) in the upper portions of the soil profile. Drainage of reforestation sites can improve height (Lieffers and Rothwell 1986; Wells and Warren 1997), diameter (Seppälä 1969), and root growth (Adams et al. 1972; Lieffers and Rothwell 1986) of recently planted spruce seedlings. The frequency of ditching across poorly drained sites can also influence seedling performance, with the shoot growth of black spruce seedlings declining as the spacing of the ditches across the site increases from 3 to 15 m (Wells and Warren 1997). Also, distance of the planting spots from the drainage ditch can affect seedling performance; black seedlings had improved shoot growth when planted 5 m from the ditch, while seedling performance was not improved when planted at further distances from the ditch (Roy et al. 1999). The frequency of ditching and the location of planting spots from the drainage ditch must be properly determined to ensure that adequate drainage from the upper portion of the soil profile provides microsites that can improve seedling growth.

The improved aeration that occurs within the soil profile in the years after ditching can create conditions favorable for microbial activity, which can cause a subsequent release of nutrients (Sivola et al. 1985). This phenomenon has resulted in an increase in foliar N, P, and K concentrations of black spruce needles over a number of years after site drainage (Mugasha et al. 1993). The level of N mineralization after ditching is dependent upon the inherent fertility of the organic substrate (Wells and Williams 1996). Sites with low fertility may require nutrient amendments with fertilizers (e.g., P: Dickson 1971), further soil aeration through tilling (Wells and Williams 1996), or the combination of both practices (Wells and Warren 1997) to provide an adequate mineralization of N for growth of peatland spruce plantations. Fertilization of black spruce with N, P, and K on drained sites resulted in increased needle concentrations of these nutrients, and elevated N concentrations resulted in a concomitant increase in needle mass (Mugasha et al. 1993, 1999). This indicates that seedlings planted on drained low fertility sites would respond to fertilization. If ditching is going to be used as a site preparation practice, fertility of the organic substrate needs to be determined to ensure that the silvicultural prescription for low fertility sites also includes fertilizer amendments.

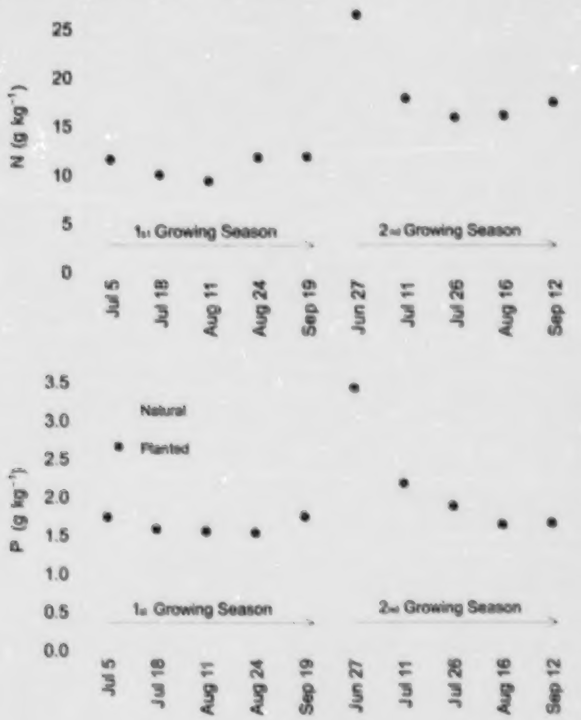
Soil water conditions created through ditching can change considerably after as little as 2–3 years due to peatland subsidence (Rothwell et al. 1996; Prévost et al. 1997). This collapse of surface peat soils through physical settling and (or) increased organic matter decomposition has the potential to change the hydrologic, thermal, and aeration properties of the soils that spruce seedlings are planted into on low-lying reforestation sites. Roy and associates (1999) found that, 2 years after ditching, this phenomenon caused a comparable depth of the aerobic layer in the soil surface horizons between planting spots located from 5 to 60 m from the drainage ditch. Soil surface subsidence may create a situation where ditching only provides a short-term improvement in aeration in the upper portions of the soil profile of northern latitude reforestation sites prone to flooding.

5.4.6 Fertilization

The nutrient cycle of a reforestation site is directly affected by harvesting of the aboveground tree biomass. The nutrient losses that occur from northern latitude spruce sites due to conventional logging practices are replaced, in part, by natural occurrences such as nutrient deposition through precipitation and the natural weathering of site organic matter and parent material (Section 1.5.2). However, on sites with marginal fertility, conventional logging practices may deplete nutrient reserves to an extent that fertilization is required to maintain productivity of the second rotation (Weetman and Webber 1972). Thus, fertilization can be considered as a necessary silvicultural practice within certain forest regeneration programs.

Recently planted seedlings are more likely to have a lower nutrient status as they begin to grow during the establishment stage. This occurs because a spruce seedling's nutrient status and subsequent growth are tied to the internal mobilization of nutrients to sites of active growth and the external uptake of nutrients from the soil (Section 3.6.1). Recently planted seedlings are likely to have a low level of nutrient uptake from the soil until new root and mycorrhizal development can balance nutrient demand that occurs due to active growth. As a result, newly planted spruce seedlings can have a lower N and P status during the first growing season after field planting, indicating the occurrence of nutrient stress (Fig. 5.4.6). Black spruce seedlings cannot only have lower levels of N and P, but also lower levels of a number of other macronutrients (i.e., K, Ca, Mg) and micronutrients (i.e., Cu, Fe, Mn, Zn) during the first growing season after transplanting (Kim et al. 1999). Improved N and P status during the second growing season in the field indicates that planted seedlings are better able to acquire soil nutrient resources as root systems develop out into the surrounding soil system.

Fig. 5.4.6. Growing season N and P concentrations of needles (current and older) of planted container-grown and naturally regenerated black spruce seedlings over two growing seasons on a boreal reforestation site in central Quebec (adapted from Munson and Bernier 1993). There were significant differences ($p < 0.001$) in N and P concentrations between container-grown and natural seedlings during the first growing season after planting the container-grown seedlings.



This physiological phenomenon of a lower internal nutrient status, due to a dilution of the existing internal nutrient pool as young seedlings begin to grow, is the reason why fertilization at planting can be important for the establishment of spruce seedlings.

Performance of spruce seedlings on the reforestation site in terms of fertilization is addressed from two silvicultural perspectives. First, the application of fertilization treatments in the nursery can be used to "nutrient-load" seedlings. Second, fertilization treatments can be applied around seedlings at the time of or after planting. Both these approaches are intended to improve the subsequent seedling field performance. Interestingly, these two approaches have resulted in varying degrees of success in seedling performance on reforestation sites.

5.4.6.1 Nutrient loading in the nursery

Nutrient loading is a nursery fertilization practice that builds up plant nutrient reserves by inducing luxury consumption of nutrients towards the end of the nursery cultural phase when seedlings have ceased shoot growth in the nursery (Section 5.1.1.3). These additional nutrient reserves are then remobilized to locations of new growth during the subsequent growing season (Section 3.6.1). In most instances, this practice of preplant nutrient loading of spruce seedlings improves subsequent field performance (Table 5.4.6.1). In all of these studies, height growth after planting was improved by nutrient loading.

Greater shoot and root production in recently planted seedlings that have been nutrient-loaded is attributed to a greater build-up of mineral nutrient reserves (van den Driessche 1985). For example, white spruce seedlings treated with late-season N after bud formation had greater root growth capacity just prior to planting and subsequently greater shoot growth and survival during the first field season (van den Driessche 1992). In another example, nutrient-loaded black spruce seedlings had greater root growth over the first year and greater shoot growth over the first and second years on a reforestation site (Fig. 5.4.6.1). In addition, exponential fertilization (i.e., increased nutrient additions to match exponential growth) promoted growth of black spruce seedlings during the first field season (Timmer et al. 1991). This was attributed to a lower shoot/root mass ratio at planting and more effective nutritional adaptation of seedlings to the field environment (Timmer et al. 1991). The benefit of exponential fertilization increases with harshness of the planting site.

Black spruce seedlings that are nutrient-loaded have increased nutrient uptake after field planting, with a greater response on infertile sites (Timmer and Aidelbaum 1996). This was attributed, in part, to greater root development in the field, which resulted from the nutrient-loading treatment in the nursery (Malik and Timmer 1996, 1998). In addition, nutrient-loaded black spruce seedlings have good growth and are effective on reforestation sites with high levels of competition (Imo and Timmer 1999). Timmer and Aidelbaum (1996) speculated that nutrient loading may confer an exploitative trait which triggers a different nutrient utilization strategy, enhancing the competitive ability of seedlings to

Table 5.4.6.1. Influence of nursery fertilization on the field performance of spruce planting stock.

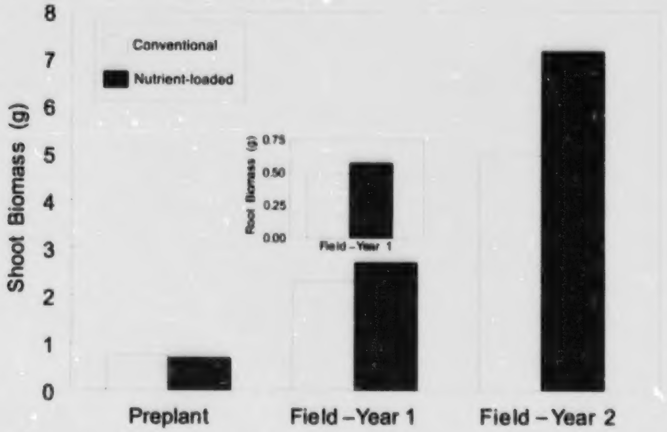
Spruce species	Stock type[a]	Field age	Fertilizer treatment	Survival[b]	Height or root growth[b]	Reference
White	1+0 C	1	N	↑	↑ Height and root	van den Driessche 1992
	1.5+1.5 BR	5	N, P, K	⊙	↑ Height	Mullin and Bowdery 1977
	3+0 BR	1	N	⊙	↑ Height and root	McAlister and Timmer 1998
Interior	2+0 BR	1	N	na	↑ Height	Donald and Simpson 1985
	2+0 BR	1	N	na	↑ Height and root	Simpson 1988
Sitka	2+0 BR	3	N	↑	↑ Height	van den Driessche 1984
	2+0 BR	4	N	⊙	↑ Height	Benzian et al. 1974
Black	1+0 C	1	N	na	↑ Height	Timmer and Munson 1991
	1+0 C	1	N, P, K	na	↑ Height	Malik and Timmer 1995
	1+0 C	2	N, P, K	na	↑ Height and root	Malik and Timmer 1996, 1998
	1+0 C	1	N, P, K	na	↑ Height	Imo and Timmer 1999
Norway	2+0 BR	3	N	⊙	↑ Height	Benzian et al. 1974

[a] C represents a container-grown stock type, and BR represents a bare-root stock type.

[b] Survival or growth response is defined by no effect (⊙) or a positive effect (↑) on performance. If measurement was not taken, it is indicated as not applicable (na).

access site nutrients after planting. Traditionally, spruce seedlings reallocate internal nutrient reserves from older tissue to new growth rather than depending upon absorption of nutrients from the soil (Section 3.6.1). In contrast, early successional species grow rapidly and have high rates of nutrient absorption throughout the growing season (Section 5.5.4). This puts spruce seedlings at a competitive disadvantage in the initial nutrient availability cycles of a disturbed ecosystem. Timmer and Aidelbaum (1996) suggested that preconditioned spruce

Fig. 5.4.6.1. Shoot and root biomass of nonloaded and nutrient-loaded black spruce seedlings planted on a reforestation site in northwestern Ontario (48.49° N lat.) (adapted from Malik and Timmer 1996).



seedlings can use this exploitative trait to more effectively compete for limited site nutrients on reforestation sites with heavy competition.

Increasing nutrient reserves through nursery fertilization, and thus increasing internal nutrient cycling (Section 3.6.1), is considered a very energy-efficient approach to nutrient acquisition for the seedling, compared to the uptake of nutrients from the soil (Binkley 1986). However, any potential benefit of increased fertility in the nursery in terms of improved seedling performance in the field is short-lived. Nutrient reserves in spruce seedlings decline after planting, due to dilution in tissue nutrient concentrations if external nutrient sources cannot meet the demands of new growth (Munson and Bernier 1993). Thus, the most important lasting effect of nutrient loading is that it promotes seedling shoot and root growth after planting. This improved growth results in enhanced seedling competitiveness due to exploitation of above- and below-ground resources from neighboring vegetation (Malik and Timmer 1998).

In an interesting finding, Sullivan and Moses (1986) found that 70–100% of the reported mortality of nursery-grown white spruce seedlings could be attributed to snowshoe hares (*Lepus americanus* Erxleben) feeding on seedlings during the first year after planting on reforestation sites in central British Columbia. Further investigation led to the conclusion that snowshoe hares prefer to feed on nursery-grown seedlings because of their higher nutritional value (i.e., higher N content) than naturally regenerated white spruce seedlings (Rodgers et al. 1993). A similar phenomenon occurs in Norway spruce where the frequency of browsing by roe deer (*Capreolus capreolus* L.) is higher in seedlings that have higher N concentration (Bergquist and Örlander 1998). It has been hypothesized that many herbivores preferentially feed on vigorous plants or plant parts (Price 1991). Increasing nutrient reserves, through nursery fertilization, may increase browsing damage incurred by spruce seedlings that are planted on reforestation sites where large populations of herbivorous animals are present.

5.4.6.2 Field site fertilization

Field application of fertilizers can be used to improve the performance of field-planted seedlings. This silviculture treatment can have beneficial effects because newly planted seedlings have restricted root development to access soil nutrients and because northern reforestation sites can present unfavorable soil nutrient conditions (Section 1.5.2). However, spruce seedling performance in response to field site fertilization is variable (reviewed by Brockley 1988; van den Driessche 1991*d*) (Table 5.4.6.2). In a number of these studies, spruce seedling performance, primarily height growth, was enhanced by the application of fertilizers to the field site. One of the largest reported increases in height growth was 15–20 cm for interior spruce seedlings in response to field fertilization (Brockley 1988). When a positive growth response occurs after field site fertilization, the effect may be short-lived. Paquin and associates (1998) found a positive response in increased height growth of black spruce seedlings for 2 years after planting, although no beneficial effect occurred during the third and fourth years after fertilizer application. In other instances, there was no enhancement of shoot growth with the application of fertilizers to the field site. These findings indicate the variable, as well as the ephemeral, nature of field site fertilization within forest regeneration programs.

Variability in seedling response to field fertilization is attributed to a number of factors (Sutton 1982; Brockley 1988). First, there is an inherent variation in fertility levels of the soils for any particular northern latitude reforestation site (Section 1.5.3). Second, another specific northern latitude reforestation site environmental factor (e.g., soil temperature, soil water, light), rather than site nutrition, could be the primary factor limiting seedling growth. Third, N is normally bound up in the forest floor, in organic layers and within the vegetation, and is not available to seedlings except through mineralization and nitrification processes. These processes can occur as a result of site disturbance due to harvesting practices (Section 1.5.2), resulting in higher N concentrations in seedlings planted in clear-cut areas compared to seedlings occurring naturally in adjacent mature spruce forests (Gordon and Van Cleve 1987). Nitrogen-saturated soil conditions that can occur on reforestation sites may limit the beneficial effects that can occur because of field fertilization. Fourth, field site fertilization can stimulate growth of competing vegetation. For example, field fertilization stimulated weed growth, resulting in the suppression of black spruce seedlings on a high-competition site, while field fertilization stimulated the growth of black spruce seedlings on a low-competition site (Fig. 5.4.6.2). Slow-growing later-climax species such as spruce typically grow in infertile environments and are more likely to survive low nutrient availability. These slow-growing climax species are not highly responsive to nutrient addition so that if fertilized they accumulate nutrient reserves rather than show large increases in growth rate (Chapin 1983). Also, recently planted seedlings have restricted root development out into

Table 5.4.6.2. Influence of fertilization at the time of planting on the field performance of spruce planting stock.

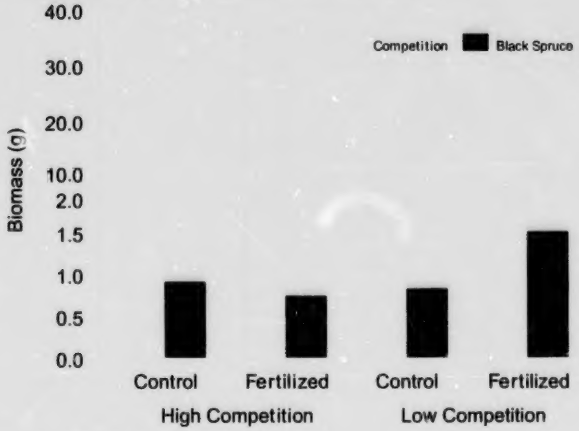
Spruce species	Stock type[a]	Field age (years)	Fertilizer treatment[b]	Survival[c]	Height growth[c]	Reference
White	2+2 BR	1 and 2	N_{br}	na	⊙	White 1960
	3+0 BR	5	N, P_{br}	na	↑	Swan 1965
	3+0 BR	1 and 2	N, P, K_{br-slr}	na	⊙ or ↑	Brand and Janas 1988; Brand 1990
		4			⊙	Munson et al. 1993
	3+0 BR	2	N, P, K_{sp}	↓	⊙	Sutton 1982
	2+2 BR	1 and 2 / 7	N_{br}	na	↑ / ⊙	Sutton 1995
Engelmann	2+0 C	1–3	N, P, K_{sp}	⊙	↑	Maze and Vyse 1993
Interior	2+0 BR 1+0 C	1 and 2	N, P, K_{br-slr}		⊙ and ↑ ↑ and ↑	Burdett et al. 1984
	1+0 C	1	N, P, K_{sp}	⊙	⊙	Sutherland and Newsom 1988
	1+0 C	7	N, P, K_{sp}	↓	⊙	Simpson and Vyse 1995
Sitka	1+0 C	3	N, P, K_{sp}	na	↑	Arnott and Brett 1973
Black	1+0 C	1 and 2	N_{sp}	na	⊙ or ↑, depending on site	Munson and Timmer 1989*b*
	1+0 C	2	P, K_{sp}	na	⊙ or ↑, depending on site	Wells and Warren 1997
	2+0 C	1 and 2, 3 and 4	N, P, K_{sp}	na	↑, ⊙	Paquin et al. 1998
Norway	2+2 BR	5	N, P, K_{sp}	⊙ or ↓	⊙	Leikola and Rikala 1974

[a] C represents a container-grown stock type, and BR represents a bare-root stock type.

[b] Fertilizer treatments are defined by broadcast (br), broadcast – slow release (br–slr), or spot fertilization (sp).

[c] Survival or growth response is defined by no effect (⊙) or a positive (↑) or negative (↓) effect on performance. If measurement was not taken, it is indicated as not applicable (na).

Fig. 5.4.6.2. Aboveground biomass of neighboring noncrop vegetation and black spruce seedlings after one growing season on high- (i.e., presence of *Alnus rugosa*) and low- (i.e., presence of *Pleurozium* mosses) competition sites that were either fertilized (granular fertilizer 20:20:20 N:P:K broadcast at 350 kg N ha^{-1}) or not fertilized (control) (adapted from Imo and Timmer 1999).



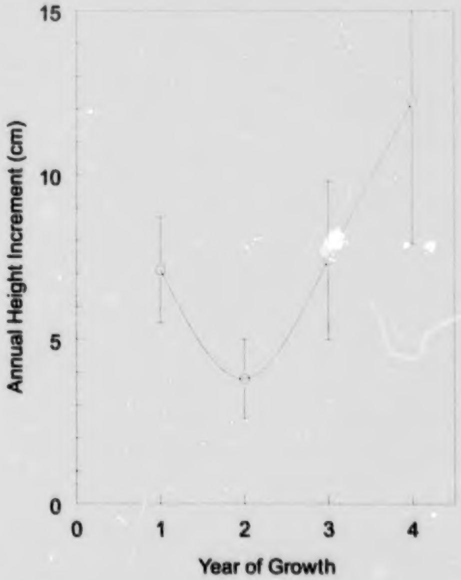
the soil profile during the establishment stage. It must be recognized that broadcast fertilization distributes fertilizer across the entire site. Recent work has found that after two growing seasons, white spruce seedlings utilize <1% of N fertilizer applied by broadcast application at the time of planting (Staples et al. 1999). This indicates that broadcast fertilization can be a very inefficient method to apply nutrients to the intended crop of spruce seedlings. On the other hand, early successional species are more efficient than spruce seedlings in accessing site available nutrients. Such rapidly growing species respond to nutrient additions with an accelerated growth rate rather than an accumulation of nutrient reserves (Chapin 1983). Therefore, fertilizing spruce seedlings after they have a well-developed root system may allow them to take up nutrients supplied through fertilization from the soil and show a positive growth response in future years compared to the immediate growth response of pioneer species.

Field site fertilization can cause rapid development of competition during the early stages of stand establishment, with early successional species maintaining a competitive advantage over recently planted spruce seedlings under favorable conditions. Due to the variability of success in past field fertilization programs to consistently enhance spruce seedling performance on reforestation sites, this silvicultural practice is considered an expensive and an inefficient approach to supplying nutrients to conifer seedlings (Brockley 1988). Alternative application approaches may need to be considered to increase the chances of successful field site fertilization. One approach may be to place the fertilizer in a hole within very close proximity of, although not touching, the roots, which avoids the problem of soluble nutrient salts causing root damage when they are placed directly in the planting hole (van den Driessche 1991*d*). This approach can result in an increase in height and diameter growth of recently planted conifer seedlings (reviewed by van den Driessche 1991*d*). Another approach to use in fertilizing spruce seedlings may be to incorporate controlled-release fertilizer products into the growing media of the container plug. Placing fertilizer within very close proximity of the roots, by either of these methods, puts the fertilizer where seedlings can take advantage of the nutrient supply, while keeping it away from competing vegetation. If field site fertilization is going to be considered a consistently viable silvicultural practice, foresters need to develop innovative approaches that ensure the seedling, rather than the competition, receive the benefit of applied nutrients.

5.4.7 Growth check

Growth check, or planting check, is a phenomenon that occurs in spruce seedlings and has long-term implications on plantation performance. Numerous studies have reported restricted field growth of recently planted spruce seedlings (Armson 1958; Mullin 1963, 1964; Eis 1966; Stiell 1976; Vyse 1981; Burdett et al. 1984; Sutton 1992). Growth check usually starts in the second year after planting and lasts for periods of 1–20 years after planting, with the normal period of growth check being 1–3 years (Fig. 5.4.7). Limited plantation performance of spruce has been attributed to a number of physiological mechanisms, including limited fertility (Sutton 1975), water stress (Grossnickle 1988*b*), and frost damage (Mullin 1963; Sutton 1992). Burdett et al. (1984) proposed that there are two

Fig. 5.4.7. Annual growth of 1+0 container-grown interior spruce seedlings on a reforestation site in central British Columbia (adapted from Vyse 1981). Seedlings were planted at year zero.



phases to growth check: (*i*) spruce seedling development is altered by water stress (Section 5.3), and (*ii*) continued limitations to seedling growth are caused by nutrient deficiencies of the site. Each of these mechanisms are examined here briefly to discern how they contribute to growth check in spruce seedlings.

Growth check of spruce seedlings has been attributed to limited fertility of the soils within the plantation. In forest soils, inorganic N changes from predominantly NH_4^+ in late successional northern latitude forest soils to mostly NO_3^- after harvesting (Section 1.5.2). Competition for available N can affect relative species performance. Pioneer species can extract nutrients rapidly from the soil solution (Chapin 1983) and use either NH_4^+ or NO_3^- as their N source (Vessey et al. 1990). White spruce discriminates against the uptake of NO_3^- and preferentially uses NH_4^+ as the main source of N (Section 3.6.1). It has been proposed that this inability of white spruce to use NO_3^- as a main source of nitrogen limits the ability of this species to be competitive on disturbed sites and is a major factor in the high incidence of plantation failure on reforestation sites (Kronzucker et al. 1997). The reduced physiological capacity of spruce species to use the most readily available N source on northern latitude reforestation sites places newly planted seedlings at a competitive disadvantage with early successional species during the plantation establishment phase.

Another example of growth check due to limited fertility is the relationship of competing vegetation with the ectomycorrhizal association found on spruce seedling root systems. Ectomycorrhizal fungi are known to enhance tree growth through an improvement in nutrient uptake (Section 5.4.8). A number of studies have reported that the litter from certain understory species is fungi-toxic, which reduces ectomycorrhizal formation on the roots of Sitka spruce (Handley 1963; Robinson 1972). The suppression of Sitka spruce growth was attributed to the direct competition between the two species for mineral nutrients or to a chemical inhibition of tree or mycorrhizal growth by the vegetation cover. This example shows how vegetation interactions could also have an effect on the growth check of spruce seedlings.

The inherent water relations of spruce seedlings during the growing season have also been suggested as a cause of growth check in young plantations. Spruce is a species that has a low level of tissue elasticity compared to pine (Section 2.1.1). Low cell wall elasticity preserves high tissue relative water content as Ψ decreases, providing tolerance to moderate and severe drought. However, low cell wall elasticity can also cause rapid development of low Ψ (Section 2.1.1), causing a loss of physiological activity (e.g., rapid stomatal closure and reduced P_n under increasing atmospheric evaporative demand or low soil water) even when the tissue has high relative water content. Thus, spruce is a species with stomata that are very sensitive to both high VPD and drought (Sections 3.2 and 3.5.2.1, respectively). Reforestation sites present an environment with a daily range in VPD and potentially low soil water that can cause stomatal closure, thereby restricting photosynthesis. This has led to the supposition that high stomatal sensitivity of spruce species to drought may be one of the reasons for growth check when seedlings are planted on reforestation sites (Grossnickle and Blake 1987*a*). White spruce uses the drought avoidance strategy of closing stomata, thereby reducing photosynthesis, to preserve high tissue relative water content when exposed to moderate and severe levels of drought stress, which enables this species to withstand potentially lethal water stress that can occur on reforestation sites. However, this drought avoidance strategy can also limit the access to photosynthates required for growth, while associated tree species (Jarvis and Jarvis 1963*a*) and early seral stage species generally have a high level of overall physiological activity and growth under similar site environmental conditions.

Growth check in spruce plantations has also been attributed to shoot damage due to frost during the growing season (Sutton 1992). White spruce has a low level of freezing tolerance during the period of active shoot growth (Section 3.7.4). Shoots of actively growing spruce seedlings can only withstand freezing temperatures of –3 to –4°C before they start to become damaged. This freezing damage can cause a reduction in physiological activity (e.g., reduced g_{wv} and P_n) and a subsequent reduction in growth (Section 3.3.1). Frosts can occur on open boreal reforestation sites at any time during the growing season (Sections 1.2.3 and 5.4.3). This combination of low freezing tolerance and the possibility of summer frost events on reforestation sites can contribute to the reduced growth found in spruce plantations.

Growth check in spruce plantations has been attributed to limited site fertility, water stress, or frost damage. Each reforestation site exposes spruce seedlings to various combinations of environmental conditions. Thus, it is very difficult to establish any one of these physiological mechanisms as the main reason that some spruce plantations show growth check. Growth check of spruce can be caused by any one or a combination of these physiological mechanisms, depending upon the limiting environmental conditions of the reforestation site.

5.4.8 Seedling–microbial interactions

The rhizosphere is a region around the roots of spruce seedlings where there is an active association with soil microorganisms. The seedling root – microbial relationship exists because the heterotrophic soil microbial populations depend upon the organic compounds (i.e., detritus, secretions, and exudates) from seedling root systems for their energy supply. As a result, this region is rather unique within the general soil system, and is a highly favorable habitat for microbial colonization and growth. The rhizosphere generally extends a few millimeters or less around the roots, although it can extend up to 1 cm in sandy soils. The surface of the root system is the rhizoplane. The interactions between seedling roots and soil microorganisms take place within the rhizosphere and rhizoplane, which can affect spruce seedling growth and performance. This section briefly discusses two microbial groups, ectomycorrhizal fungi and plant growth promoting bacteria, that are currently being applied to spruce seedlings in an attempt to enhance performance on reforestation sites.

Mycorrhizae is a term meaning "fungus root"; this is an association that occurs between mycorrhizal fungi and roots of spruce seedlings. Ectomycorrhizal fungi are characteristically found on spruce species (Harley and Smith 1983). The appearance of ectomycorrhizal fungi is distinguished by a sheath of fungal tissue around the short lateral and sometimes longer lateral roots of trees (Bowen 1965; Harley 1969). The fungal sheath is usually connected with the soil by hyphae which radiate out into the soil complex and increase the absorbing area of the root system (Went and Stark 1968). Depending upon the specific mycorrhizal fungi, these hyphae can range from sparse, nearly invisible threads to prolific wefts and root-like strands that are critical for the transport of nutrients and water (Castellano and Molina 1989). Hyphae also develop intercellularly into the root cortex, extending between the epidermal cells and the first few layers of the cortex (Bowen 1965; Harley 1969). These intercellular hyphae are commonly referred to as the "Hartig net" and together with the fungal mantle around the roots are the major distinguishing characteristics of ectomycorrhizal fungi (Harley and Smith 1983).

Ectomycorrhizal fungi enter into a symbiotic relationship with the host tree species. The rate of ectomycorrhizal development is directly related to macronutrient levels, intensity of sunlight in relation to photosynthetic activity, soil water content, temperature, soil oxygen content, and competition from other microorganisms (Harley 1969; Slankis 1974). Ectomycorrhizal development is also influenced by vitamins (i.e., thiamine), amino acids, and carbohydrates, which are derived from the roots (Melin 1954; Harley 1969). Whether or not a symbiotic relationship is formed between the tree species and ectomycorrhizal fungi depends upon the environment and the ability of the fungi to induce and maintain a specific physiological and metabolic state in the root, which is conducive to the mycorrhizal fungi.

Ectomycorrhizal fungi enhance tree growth, in part, through the improvement in nutrient uptake. Improved nutrient uptake occurs due to nutrients being absorbed through the fungi and passed along into the root system of the host tree species. Studies have shown that ectomycorrhizal fungi increase the uptake of macronutrients such as N, P, K, and Ca (Harley and Smith 1983). Increased nutrient absorption was partly explained by Hatch (1937) as being due to the physical increase of the effective surface area for absorption caused by ectomycorrhizal infection around the root and the development of hyphal strands into the soil. These hyphal strands can take up nutrients from the soil and translocate these ions over long distances where they accumulate within the mycorrhizal root tips. Nutrient absorption by ectomycorrhizal fungi is believed to be similar to the same metabolic processes found in roots (Harley and Smith 1983). (Details on nutrient uptake in spruce seedlings are found in Section 2.3.1.)

Ectomycorrhizal fungi are also believed to enhance tree growth through improvement in the absorption of soil water. Early field studies found seedlings infected with ectomycorrhizae seem to be more resistant to drought stress than uninfected seedlings (Cromer 1935; Harley 1940). Possible explanations for this phenomenon are the following: first, the addition of ectomycorrhizal hyphal strands increases the absorbing area of the root system; second, fungal hyphae may penetrate smaller soil pores than root hairs; and third, hyphal strands from the fungus–root association are connected to the soil particles, which prevents the shrinkage of soil away from the fungus–root surface and thus improves root–soil contact (Reid 1979). Findings to substantiate this improved water uptake phenomenon through the fungus–root association are mixed, with some studies finding increased water movement through the SPAC (Dixon et al. 1983; Lamhamedi et al. 1992) and improved drought resistance (Parke et al. 1983) in field-planted seedlings, while other work reporting that this association increased the resistance of water movement along the SPAC (i.e., lower shoot Ψ) (Sands and Theodorou 1978; Coleman et al. 1987) or had no influence on seedling water movement capability (Sands et al. 1982) or shoot Ψ response to field drought (Diebolt and Mudge 1987). (Details on water movement through the SPAC are found in Section 2.1.2.) Where ectomycorrhizal fungi are effective in improving water uptake, it seems that these fungi have large mycelial strands that radiate out into the soil and increase water flow from the soil to the roots (Lamhamedi et al. 1992). It is possible that certain ectomycorrhizal fungi, which have large and extensive root-like strands of hyphae that radiate out into the soil, can confer improved drought avoidance in seedlings. Further work on the water relations of spruce seedlings infected with specific ectomycorrhizal fungi are required to define their influence on the seedling water balance.

Some soil bacteria colonize the rhizosphere and rhizoplane regions of plants. These rhizosphere bacteria do not actually infect the root systems of spruce seedlings, rather they exist in the region on and surrounding the seedling roots. These rhizosphere bacteria utilize root exudates, such as organic compounds, as their energy supply. Rhizosphere bacteria can typically reach population sizes that are 10–100 times greater than those found in the soil further away from the root system. Some rhizosphere bacteria are also able to gain entry into the root system and are considered endophytic bacteria.

One group of bacteria, known as plant growth promoting rhizobacteria (PGPR), have the capability to colonize root systems and stimulate plant growth (Kloepper and Schroth 1978). The actual mechanisms by which PGPRs stimulate plant growth are still open for speculation, although a number of mechanisms have been proposed, with plant growth promotion by bacteria occurring through either direct or indirect means. The direct means of plant growth promotion by PGPR is through the production of a metabolite that itself is stimulatory to the plant (Kloepper 1993). Possible mechanisms of direct plant growth promotion by PGPR are the following: (*i*) root-associated nitrogen fixation, (*ii*) the production or inhibition of hormones, (*iii*) enhanced nutrient availability (e.g., P solubilization, NO_3^- availability, S oxidation), (*iv*) increased root permeability, and (*v*) improved resistance to root pathogens (reviewed by Chanway 1997). The indirect means of plant growth promotion by PGPR is through the bacteria affecting other factors in the rhizosphere, which in turn enhance plant growth

Table 5.4.8. Performance of spruce seedlings after being inoculated with either ectomycorrhizal fungi or plant growth promoting rhizobacteria.

Spruce species	Inoculated microorganism	Experimental condition	Shoot growth[a]	Reference
White	Ectomycorrhizae	Greenhouse	⊙	Shaw et al. 1982
	Soil bacteria	Reforestation site	↑ or ⊙, depending upon bacterial species and site location	Reddy et al. 1997
Engelmann	Ectomycorrhizae	Afforestation site	↑ or ⊙, depending upon mycorrhizal species	Grossnickle and Reid 1982
	Ectomycorrhizae	Greenhouse	↑	France and Cline 1987
	Ectomycorrhizae	Greenhouse	↓	Hunt 1992
		Reforestation site	⊙	
Sitka	Ectomycorrhizae	Greenhouse	⊙	Shaw et al. 1982
	Ectomycorrhizae	Reforestation site	↓, ↑, or ⊙, depending upon mycorrhizal species	Shaw et al. 1987
	Ectomycorrhizae	Reforestation site	⊙	Loopstra et al. 1988
Black	Ectomycorrhizae	Greenhouse	⊙	Gagnon et al. 1988
	Ectomycorrhizae	Reforestation site	↓ or ⊙, depending upon mycorrhizal species	Browning and Whitney 1992, 1993
Interior	Soil bacteria	Greenhouse	↑ or ⊙, depending upon bacterial species	Chanway et al. 1989
	Soil bacteria	Greenhouse	↑ or ⊙, depending upon bacterial species	O'Neill et al. 1992
	Soil bacteria	Reforestation site	↑ or ⊙, depending upon bacterial species	Chanway and Holl 1993
	Soil bacteria	Greenhouse	↑	Shishido and Chanway 1999

[a] Growth response is defined by no effect (⊙) or a positive (↑) or negative (↓) effect on shoot growth performance.

(Kloepper 1993). Possible mechanisms of indirect plant growth promotion by PGPR are the following: (*i*) increased number of ectomycorrhizal root tips, (*ii*) suppression of deleterious rhizobacteria (reviewed by Chanway 1997), and (*iii*) inhibition of root pathogens (P. Axelrood, personal communication). Determining the precise mechanism that causes plant growth promotion by PGPR can be difficult because individual strains may possess characteristics consistent with several mechanisms (reviewed by Chanway 1997).

Both ectomycorrhizal fungi and PGPR have been applied to spruce seedlings in an attempt to promote their performance on reforestation sites. Seedlings are inoculated with these microorganisms while in the nursery or just prior to planting. Both ectomycorrhizal fungi and PGPR have been found in some cases to promote spruce seedling performance in greenhouse experiments and in the field, while in other cases they have been found to have no beneficial effect on seedling performance (Table 5.4.8). Reasons for variability in the promotion of spruce seedling growth by soil microorganisms can be attributed to the inoculant delivery system, host–microorganism specificity, the interaction of spruce seedlings or the inoculated microorganism with the indigenous soil microorganisms found on the reforestation site, and site environmental conditions. The interaction of the seedling–microorganism relationship can be affected by their individual as well as interdependent response to site environmental conditions and soil properties. In many instances, the inoculated ectomycorrhizal fungi or PGPR are not adapted to planting site conditions. Thus, they cannot compete with the indigenous soil microorganisms. The use of ectomycorrhizal fungi and PGPR as a nursery inoculation treatment has the potential to benefit spruce seedling performance during the field establishment phase. However, the seedling–microorganism relationship does not always yield improved field performance. This variability in performance needs to be recognized when considering whether to integrate soil microorganism inoculants into a forest regeneration program.

5.5 Effects of competing vegetation in the transition phase

Competing vegetation on reforestation sites can affect regeneration practices during the transition phase of plantation development. The transition phase is defined as a period when competing vegetation begins to reinvade the reforestation site and impose limitations on seedling performance (Fig. 5). This is also the phase when the influence of the original stock type or nursery cultural treatment on seedling performance usually starts to fade. Thus, in the transition phase, the seedling responds to site environmental conditions in relation to competing vegetation.

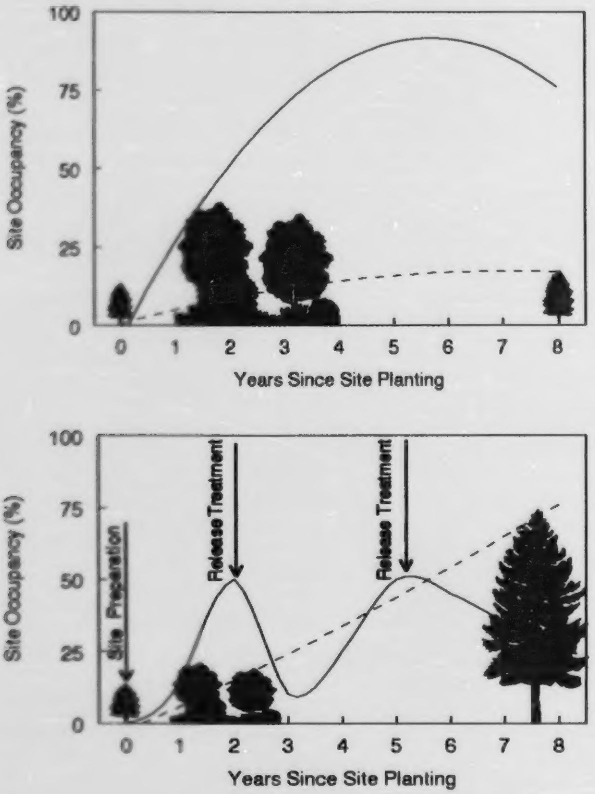
Silvicultural practices are intended to improve site access for newly established seedlings by reducing or rearranging slash and (or) ameliorating adverse forest floor, soil, above- and below-ground vegetation structure, or other site biotic factors (Daniel et al. 1979). Silvicultural practices that alter the site vegetation structure include application of a silvicultural system, site preparation, and release and improvement cuttings. The following discussion (Section 5.5) centers on site preparation practices and release treatments used on reforestation sites created through clear-cutting harvest practices, although appropriate examples from other silvicultural systems are included. The effects of silvicultural systems on site environmental conditions, competing vegetation, and spruce seedling performance are discussed elsewhere (Section 5.6).

Vegetation composition and structure on the site are removed or altered by the use of herbicides, prescribed burning, and mechanical or manual techniques. It is beyond the scope of this discussion to examine specific differences in these vegetation management techniques. These silvicultural practices are conducted to create a proper environment for the establishment and growth of seedlings. This discussion focuses on how these practices affect the ecophysiological response of spruce seedlings. Only the use of herbicides as a vegetation management tool is singled out for separate discussion. The influence of herbicides on the ecophysiological processes of spruce seedlings is the focus of this discussion (Section 5.5.5).

Harvesting is a disturbance, resulting in the redistribution and altered availability of site resources such as [illegible], water, and nutrients (Section 1). The harvesting of the overstory alters the normal successional process and creates reforestation sites that are in various secondary successional stages (Oswald 1990; Wagner and Zasada 1991). The resulting successional development is, in part, dependent upon the type, degree, and timing of the harvesting practice, which causes an alteration of species composition and spatial distribution. Plant succession following harvesting is also affected because the soil substrate is left relatively intact. This leaves the reforestation site with all of the associated microfauna and microflora, as well as subsurface organs (roots, rhizomes, and stumps) that give species of tree, shrubs, grasses, and forbes the ability to rapidly reoccupy the site (Keenan and Kimmins 1993). If left unchecked, these secondary successional species can rapidly occupy the site, thus limiting the performance of planted spruce seedlings (Fig. 5.5). Competition for reforestation site resources is one of the major factors limiting the successful establishment and growth of spruce seedlings (reviewed by Dobbs 1972; Coates et al. 1994) (e.g., Alm 1974; Mullin 1975; Eis 1981; Warren et al. 1987; Brand and Penner 1990; LePage and Coates 1994; Wagner et al. 1996) and conifer seedlings in general (Gjerstad et al. 1984; Sutton 1985; Radosevich and Osteryoung 1987).

Regeneration silvicultural practices provide a means for directing the course of the secondary successional process on reforestation sites through the addition of desirable plant species, such as planting conifer seedlings, and the removal or suppression of undesirable species (Wagner and Zasada 1991). A generalized example of how regeneration practices can alter development of the vegetation complex and lead to the improved performance of planted spruce seedlings is shown in Fig. 5.5. The removal of competing vegetation immediately after planting and keeping the vegetation in check allows planted seedlings better access to site resources, thereby improving spruce seedlings survival and growth (Lund-Høie 1984; Wood and von Althen 1993; Wagner et al. 1999), and benefits conifer seedlings in general (Stewart et al. 1984). Control of vegetation on reforestation sites enables spruce seedlings to effectively utilize site resources, grow faster, and occupy the site within a shorter time frame, which ultimately ensures successful plantation establishment.

Fig. 5.5. Conceptual changes in the reforestation site occupancy for both secondary successional species (solid line) and newly planted conifer seedlings (dashed line), depending upon whether site preparation and release treatments were or were not used to alter the allocation of site resources when seedlings were planted.



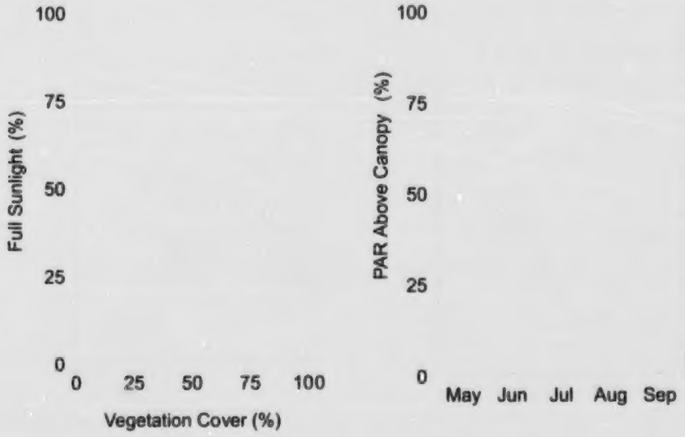
Site limiting environmental factors such as low light, cold temperatures in the rooting zone, limited soil water, and nutrient deficiency have been suggested causes for the reduction in spruce seedling performance on northern latitude reforestation sites in relation to competing vegetation. These are some of the same environmental parameters that influence the ecophysiological performance of spruce seedlings (Section 3). These environmental constraints commonly occur in field plantations of spruce seedlings in boreal and cool temperate regions and can be ameliorated by the removal of vegetation. At the same time, competing vegetation creates microclimates which alter a combination of environmental factors. Therefore, it is difficult to ascribe any single environmental variable as the sole factor in limiting spruce seedling performance on a reforestation site. It is necessary to recognize this when attempting to define limitations to spruce seedling performance. In the following discussion, examples are presented to examine the effects of competing vegetation with respect to each of the above environmental factors. This discussion also examines how competing vegetation limits the performance of spruce seedlings.

5.5.1 Light

On a reforestation site, recently planted seedlings can be exposed to full sunlight prior to the occupation of the site by fast-growing early seral stage species. Once the early seral stage species begin to occupy the site, competition influences the amount of solar radiation reaching the seedling and surrounding soil surface (Fig. 5.5.1*a*). Height, density, and leaf orientation of vegetation cover has a direct influence on the interception of light reaching the seedling (Spittlehouse and Stathers 1990; Shainsky and Radosevich 1992). As vegetation cover increases, solar radiation reaching the seedling decreases. The amount of cover changes in relation to development of foliage, with higher rates of vegetation cover occurring during the middle and end of the growing season on northern latitude reforestation sites (Spittlehouse and Stathers 1990; Brand 1991; Reynolds et al. 1997). Thus, the amount of solar radiation reaching a spruce seedling is directly related to the amount of cover and to the developmental stage of the competing vegetation (Draper et al. 1988; Comeau et al. 1993).

Competition alters the amount of solar radiation reaching the spruce seedlings, which in turn influences their physiological response and morphological development. The direct effect of reduced light on spruce seedlings is a decrease in P_n (Section 3.1) during the period of highest seasonal P_n (Section 3.9). Lower light levels also result in a reduction in the growth of spruce species. In general, both the P_n and growth of spruce seedlings is dramatically restricted at <~40% full sunlight (Section 3.1). On productive reforestation sites (i.e., high availability

Fig. 5.5.1*a*. Generalized diagram showing the influence of percent vegetation cover on light at seedling height and changes in this percentage of photosynthetically active radiation (PAR) as seasonal changes in vegetation occur around the seedling (adapted from Spittlehouse, personal communication; Spittlehouse and Stathers 1990; Stathers et al. 1990).



of water and nutrients), as the competing vegetation increases, light transmittance to the tops of black (Morris et al. 1990), Engelmann (Chen 1997) (Fig. 5.5.1*b*), or white (Brand 1991; Groot 1999) spruce seedlings decreases, resulting in a rapid reduction in seedling growth. Thus, spruce seedling growth is reduced when neighboring vegetation reaches a sufficient height and density to reduce light reaching the seedling.

The removal of competing vegetation (approximately an area of 0.6 m in diameter) around interior spruce seedlings allowed for 70% of growing season light to reach the seedling (Draper et al. 1988). In contrast, nonremoval of competing vegetation resulted in only 15% of growing season light reaching the seedlings. Scarified planting spots and sites where vegetation was annually controlled through herbicide application had 47–58% greater incoming solar radiation over the growing season, depending upon the year, when compared to planting spots where competition was not controlled (Fig. 5.5.1*c*). Removing vegetation from the immediate vicinity of a planted spruce seedling can have a dramatic effect on its exposure to growing season light.

There is a continuous change in the structure of reforestation site vegetation composition as the site goes through a normal secondary successional process. Thus, regeneration practices (in this case, planting of seedlings and vegetation removal) contribute in a number of ways to changes in site vegetation composition over time. First, shoot development of planted spruce seedlings enables them to occupy more vertical and horizontal space within the vegetation complex.

Fig. 5.5.1*b*. Relationship between aboveground stem growth of Engelmann spruce seedlings and competition index ($N = 388$). Competition index is the sum of the products of cover and height for all noncrop species. Light transmittance through fireweed – mixed shrub communities is presented at the top of the figure in relation to the competition index. The line on the graph describes the relationship between stem growth and the competition index for spruce seedlings with a needle biomass (x) of 20 g (adapted from Comeau et al. 1993).

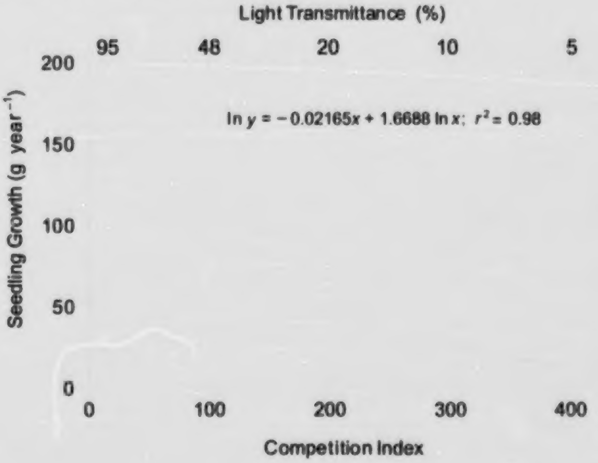
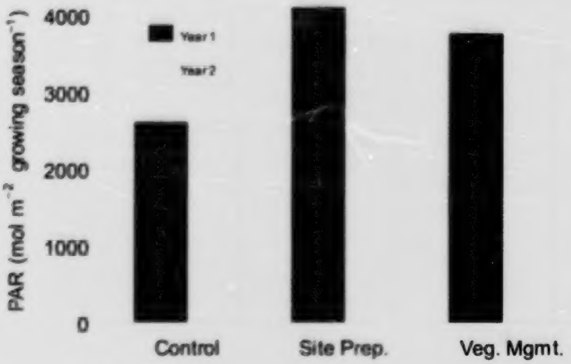


Fig. 5.5.1c. Influence of site preparation or vegetation management treatments on the amount of incoming photosynthetically active radiation (PAR) during the growing season over the first 2 years on a subboreal spruce reforestation site in central British Columbia (54° N lat.) (adapted from Brand 1991).



For example, spruce seedlings growing where there was no removal of vegetation had an increase in available growing season light because their shoots grew above the competition (Draper et al. 1988). Second, the change in structure of competing vegetation alters the degree of opening created through the original site preparation procedure. Patches that originally ranged from 0.3 to 1.3 m^2 in size decreased to between 50 and 80% of original opening size, respectively, after 4 years (Örlander et al. 1990). After openings are created, the degree of new vegetation cover within the opening is dependent upon the original opening size and the ingress of competing vegetation. These factors result in a change over time in the dynamic pattern between seedlings and competing vegetation. The pattern of incoming light can be manipulated through vegetation management techniques, and this in turn can alter the subsequent growth of planted seedlings.

5.5.2 Temperature

Both air and soil temperatures around newly planted spruce seedlings are altered by the degree of vegetation cover. Degree of vegetation cover also reduces daytime solar heating and long-wave radiative loss at night. The vegetation canopy, therefore, becomes the major location of radiative energy transfer rather than the soil surface (Sections 1.1.2 and 1.2). As a result, air temperatures around seedlings become closer to ambient, and soil surface temperatures are reduced (Spittlehouse and Stathers 1990). Depending upon the reforestation site, this can have a beneficial or detrimental effect on seedling performance.

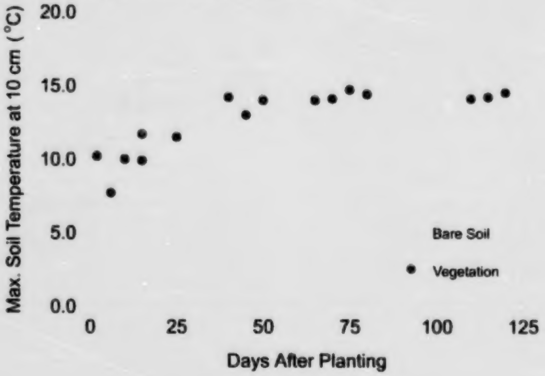
The degree of influence of vegetation cover on soil temperatures is dependent upon site location, atmospheric conditions, and physical properties of the soil profile (Section 1). Soil temperatures (at a depth of 10 cm) on boreal sites where white, Engelmann, or interior spruces normally grow range between 6 and 12°C during the growing season, when vegetation has not been removed (Tyron and Chapin 1983; Goldstein et al. 1985; Bassman 1989; Brand 1991; Coates et al.

1991; Balisky and Burton 1995). Heavy grass cover can delay thawing of the soil in the spring by up to 1 month on boreal reforestation sites (Hogg and Lieffers 1991). There are many examples where removal of vegetation cover causes an increase in growing season soil temperatures on northern latitude reforestation sites (McMinn 1982*a*; Grossnickle and Heikurinen 1989; Stathers and Spittlehouse 1990; Örlander et al. 1990; Coates et al. 1991; Hogg and Lieffers 1991; Wood and von Althen 1993; Burgess et al. 1995; Reynolds et al. 1997; Groot et al. 1997). In the example shown in Fig. 5.5.2*a*, the removal of vegetation cover consistently increased soil temperature by 2–5°C across the growing season. This daily increase can have a cumulative effect, resulting in a significant increase in soil temperatures that seedlings are exposed to over the growing season. This increase in soil temperature brought about by site preparation can last for 10 or more years in certain instances (Kubin and Kemppainen 1994). This slight, but continual increase in soil temperature can have a cumulative effect on the growth of conifer seedlings (Margolis and Brand 1990).

Site preparation treatments that remove shading vegetation cause the soil surface to warm and increase the soil temperature (Spittlehouse and Childs 1990). Also, any site preparation treatment that allows for a more efficient penetration of solar heating deeper into the soil profile, through rearrangement of the soil horizons, can increase growing season temperatures. The following are a series of examples where site preparation treatments have improved soil temperatures on northern latitude reforestation sites.

Some site preparation treatments provide a moderate increase in accumulated soil warming throughout the growing season through the removal of the vegetation cover. These treatments increase the energy exchange at the soil surface, but the intact surface organic horizon restricts the conduction of radiant energy into the soil profile due to the low level of thermal conductivity (Section 1.2.4). In the subboreal spruce zone near Prince George, B.C. (54° N lat.), the removal of competing vegetation by herbicides improved the accumulated soil

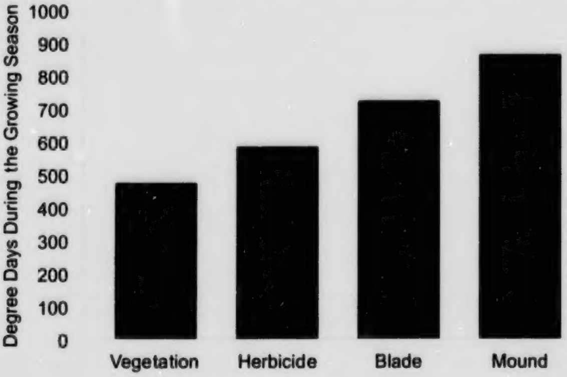
Fig. 5.5.2*a*. Maximum soil temperature over the growing season on a northern latitude reforestation site in response to competing vegetation (adapted from Grossnickle and Heikurinen 1989). Seedlings were planted in mid May.



temperature at the planting spots throughout the growing season by 23% in comparison to no vegetation removal (Fig. 5.5.2*b*). In a trial in southern Sweden, a herbicide treatment only provided a marginal increase (i.e., 2–6%) in growing season soil temperature (at 10 cm in depth) in recent clear-cuts (Nilsson and Örlander 1999). In another study in the subboreal spruce zone in British Columbia (55° N lat.), removing vegetation by broadcast burning or windrowing improved the accumulated soil temperature throughout the growing season by 15 or 12%, respectively, in comparison to no vegetation control (Yole and Kranabetter 1996*a*). Groot et al. (1997) found that mean summer soil temperature (5 cm in depth) was increased by only 2°C when vegetation was controlled by herbicides on a boreal clear-cut site. These examples show how site preparation treatments that retain the soil structure cause only a moderate increase in soil temperatures during the growing season.

Mechanical site preparation procedures increase the amount of soil warming through a reduction or alteration of the surface organic horizon. Exposure of the mineral soil increases conduction of heat into the soil profile by increasing the thermal diffusivity of the soil surface (Section 1.2.4). Mechanical site preparation treatments that produced mound or berm planting spots showed the greatest level of accumulated soil warming throughout the growing season, due to a decrease in the volumetric soil heat capacity and greater soil warming per unit of stored heat (Stathers and Spittlehouse 1990; Örlander et al. 1990; Sutton 1993; Örlander et al. 1996; Yole and Kranabetter 1996*a*; Nilsson and Örlander 1999). For example, creating planting spots in a boreal reforestation site through the removal of competing vegetation by scarification, mounding, or with a plow berm improved the accumulated soil warming throughout the growing season by 35, 53, or 75%, respectively, in comparison to no vegetation removal (Örlander et al. 1990). In another example, mechanical site preparation by either blade scarification or mounding improved growing season soil temperatures by 53 or 83%, respectively, compared to no vegetation removal (Fig. 5.5.2*b*). As well, mechanical

Fig. 5.5.2*b*. Degree day accumulation of soil temperature (at 10 cm) over the growing season on a northern latitude reforestation site in response to competing vegetation or site preparation treatments (adapted from Spittlehouse and Stathers 1990).

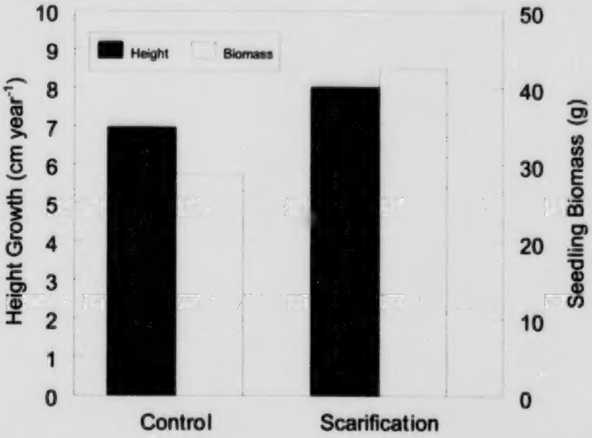


site preparation treatments on a boreal reforestation site that produced mound or berm planting spots improved the accumulated soil warming throughout the growing season by ~55% (Kubin and Kemppainen 1994). These examples indicate that mechanical site preparation treatments that produced exposed mineral planting spots or raised planting sites have an increased level of accumulated soil warming throughout the growing season.

Competition alters soil temperatures of the reforestation site, which have a direct influence on the physiological response and morphological development of spruce seedlings. Spruce seedling ability to move water through the SPAC is directly influenced by soil temperature (Section 3.5.1). In addition, spruce seedling gas exchange capacity (Section 3.5.1), ability to take up nutrients (Section 3.6.1), and subsequent morphological development (Section 3.5.1) all increase as soil temperatures increase. This is confirmed by numerous field studies where the removal of vegetation increased soil temperatures, which improved spruce seedling growth (Endean 1972; Endean and Johnstone 1974; McMinn 1982*a*; Draper et al. 1988; Coates et al. 1991; Yole and Kranabetter 1996*a*, 1996*b*) (Fig. 5.5.2*c*). Thus, the effect of vegetation cover on soil temperatures during the growing season can have major impacts on the performance of spruce plantations.

Removal of competing vegetation can also create conditions in which seedlings are exposed to greater air temperature extremes during the growing season. On sites prone to frosts, the removal of vegetation cover results in seedlings being exposed to radiative frosts (Section 1.2.3). These radiative frosts can cause physiological stress in spruce seedlings (Section 3.3.1 and 3.7.4) and reduce field performance (Section 5.4.3). As well, the removal of vegetation cover can expose seedlings to higher air and soil surface temperatures (Section 1.2.2).

Fig. 5.5.2c. The influence of scarification site preparation treatment on the growth of white spruce seedlings over the first growing season on a northern latitude reforestation site (adapted from Brand and Janas 1988). The control treatment had 1611 ± 11 growing degree days (soil temperatures >5°C), while the scarification treatment had 1884 ± 47 growing degree days.



Temperatures above ~35°C put spruce seedlings under physiological stress (Section 3.3.2) and affect their field performance (Section 5.4.4). Depending upon the field situation, the removal of the vegetation canopy in order to increase soil temperatures and improve spruce seedling growth needs to be weighed against the potential exposure of spruce seedlings to extreme air temperatures, which can cause physiological damage and potential seedling death.

5.5.3 Soil water

On certain northern latitude reforestation sites, competing vegetation can capture a large portion of the available water, creating conditions where water stress limits the performance of recently planted seedlings (Newton and Comeau 1990). This occurs because the transpiration of the vegetation cover removes soil water from the soil (top 25 cm). Root competition occurs whenever roots of different individual plants are sufficiently close to one another to modify the root environment to the detriment of either or both individuals (Sutton and Tinus 1983). In addition, competition between overlapping root systems takes place long before the tops begin to shade one another (Pavlychenko and Harrington 1935). Vegetation cover can reduce the available soil water within the effective rooting profile on reforestation sites in the northern latitude forests (Brand and Penner 1990; Burgess et al. 1995; Fleming et al. 1996; Groot et al. 1997) (Fig. 5.5.3*a*). As a result, soil water availability decreases as plant cover increases on a reforestation site (Adams et al. 1991).

Competition can reduce reforestation site soil water, which has a direct influence on the physiological response of spruce seedlings. A reduction in soil water due to vegetation cover can cause an increase in the level of seasonal water stress in newly planted white spruce seedlings over the first growing season (Fig. 5.5.3*b*). This is confirmed by other studies where an increase in plant cover resulted in a reduction in seedling Ψ across the season (Eissenstat and Mitchell

Fig. 5.5.3*a*. Soil water potential (Ψ_{soil}) changes at 10 cm in a soil profile during the growing season on a northern latitude reforestation site in response to competing vegetation (adapted from Grossnickle and Heikurinen 1989).

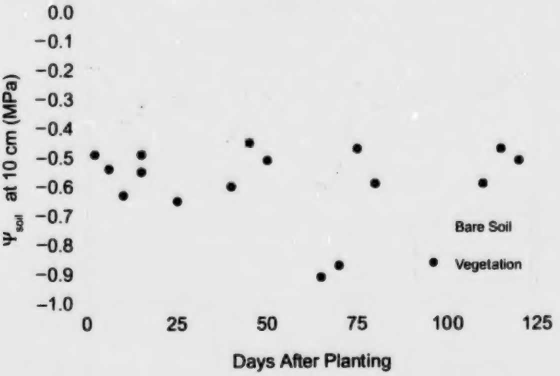
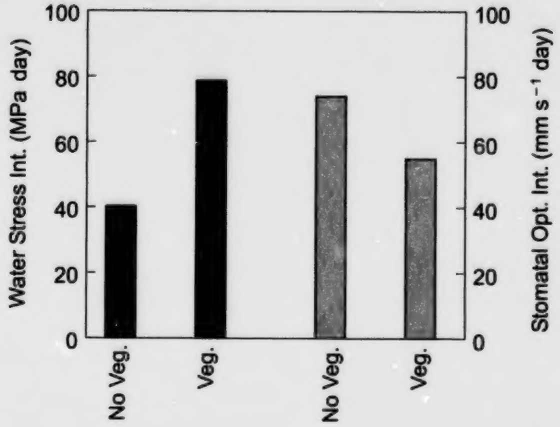


Fig. 5.5.3*b*. Water stress and stomatal optimization integrals (i.e., summation of physiological response that was measured periodically across the entire growing season) of white spruce seedlings planted on a northern latitude reforestation site, with and without competing vegetation over a 125-day growing season. The integrals represent a measure of cumulative seasonal effects on a specific physiological response (adapted from Grossnickle and Heikurinen 1989).

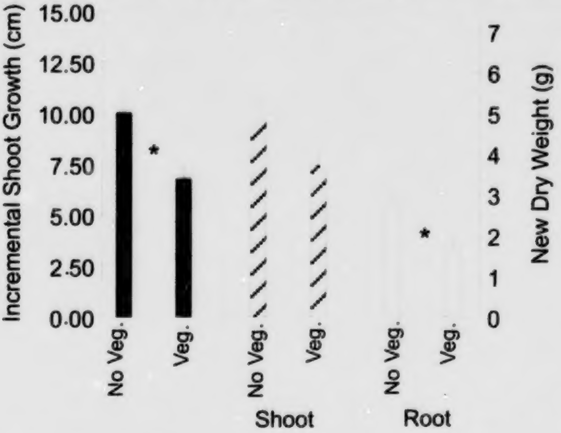


1983; Grossnickle and Reid 1984*a*; Elliot and White 1987; Petersen et al. 1988; Pabst et al. 1990; Shainsky and Radosevich 1992; Perry et al. 1994). Water stress occurs because recently planted spruce seedlings take up water mainly from the top portion of the soil profile where the roots of competing vegetation also access available water (Nilsson and Örlander 1999). The rate of stomatal opening and photosynthetic capacity of spruce seedlings are directly related to soil water, with g_{wv} and P_n decreasing as soil water declines (Section 3.5.2.1). A continual level of increased seasonal water stress due to competing vegetation with newly planted white spruce seedlings also caused a reduction in stomatal opening over the first growing season (Fig. 5.5.3*b*). This limitation of spruce seedling gas exchange response due to vegetation cover was caused by limited soil water, which increased seedling water stress.

Competition can reduce reforestation site soil water, which also has a direct influence on the morphological development of spruce seedlings. The above discussed reduction in white spruce seedling physiological activity due to competing vegetation also caused a reduction in subsequent seedling growth (Fig. 5.5.3*c*). This agrees with other work showing a reduction in conifer seedling development caused by competing vegetation lowering soil water and resulting in greater water stress in recently planted seedlings (Nambiar and Zed 1980; Carter et al. 1984; Sands and Nambiar 1984; South and Barnett 1986; Margolis and Waring 1986).

A reduction in soil water due to vegetation cover can also cause an increase in mortality of newly planted spruce seedlings over the first few growing seasons. In white spruce plantations, vegetation control conserved site soil water, resulting in 94% survival, while no vegetation control resulted in a survival rate

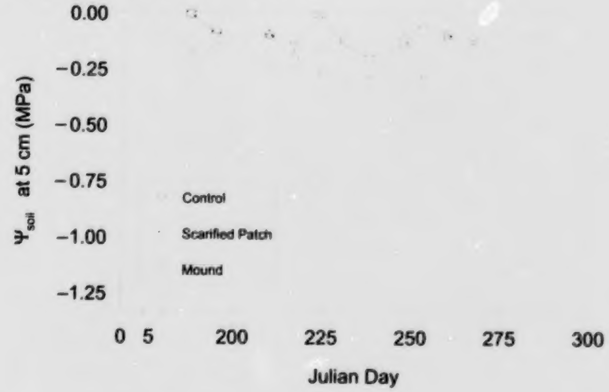
Fig. 5.5.3c. Shoot growth and new shoot and root dry weight for white spruce seedlings planted on a northern latitude reforestation site, with and without competing vegetation over a 125-day growing season. The * indicates there was a significant treatment difference ($p = 0.05$) (adapted from Grossnickle and Heikurinen 1989).



of only 22% (Sutton 1975). When Norway spruce seedlings were planted on recent clear-cuts with no site preparation, seedling survival was high, while planting of seedlings on older clear-cuts resulted in reduced survival (Nilsson and Örlander 1995). Nilsson and Örlander (1995) attributed this reduction in seedling survival to the vegetation on 2- and 3-year-old clear-cuts, depleting the available water within the effective rooting zones of newly planted Norway spruce seedlings.

Mechanical site preparation treatments that produce a mound or berm create raised planting sites that show the greatest level of accumulated soil warming throughout the growing season (Section 5.5.2). However, the benefits of raised planting spots for improved spruce seedling establishment is also dependent upon the depth of water within the soil profile. On sites where the water table is low, raised planting spots that had higher soil temperatures also dried out quickly (Örlander et al. 1990) (Fig. 5.5.3*d*). The Ψ_{soil} readings recorded for these mounded site preparation locations were low enough to cause water stress and reduced growth over 2 years in interior spruce seedlings (Bassman 1989). The rapid drying of soil in the mound has a minimal effect on seedling water status when root growth occurs beyond the mound. Norway spruce seedlings that were exposed to a drought during their third year after planting had similar seasonal Ψ values when compared to seedlings planted on sites that were herbicide-treated or had a vegetative cover (Nilsson and Örlander 1999). This occurred despite lower soil Ψ values in the mounds. Nilsson and Örlander (1999) felt that the similarity in spruce seedling Ψ values across the growing season, under different site preparation treatments, occurred because roots of the seedlings had extended beyond the mounds, and these roots could now take up water from areas in the soil having high soil Ψ. A balance must be reached between improved soil temperature and water in raised planting spots, and this balance is dependent upon the

Fig. 5.5.3d. Soil water potential (Ψ_{soil}) changes at 5 cm in a soil profile during the growing season on a northern latitude reforestation site in response to site preparation treatments (adapted from Bassman 1989).



depth to the water table during the growing season. It must also be recognized that the potential effects of raised planting spots causing water stress in planted spruce seedlings diminish as the seedlings develop roots beyond the mound.

5.5.4 Fertility

Reforestation sites generally contain a higher nutrient availability than climax forests on the same parent material (Chapin 1983) (Section 1.5.2). This occurs because mechanical logging on boreal forest sites can create drastic site conversion through disruption of the surface peat layer, thereby promoting a nutrient-enhanced substrate that promotes broad-leaved seedling establishment (Brumelis and Carleton 1988). Net N mineralization is increased on reforestation sites, which places increased quantities of nitrogen into the soil solution (Vitousek 1983). The increased N in soil solution can promote the development of newly planted seedlings, but it also promotes the development of a secondary successional vegetation complex. Development of this vegetation complex can, in turn, alter the availability of N within the soil system (Section 1.5.2). For example, on a boreal reforestation site, N availability in the soil (Örlander et al. 1996) or in white spruce needles (Gordon and Van Cleve 1987; Lieffers et al. 1993) increased after the forest canopy was removed. The availability of N then declined as vegetation regrowth reached a maximum level (Örlander et al. 1996). This creates a dynamic pattern to the N cycle on clear-cut sites as seedlings go through the transition phase of plantation establishment.

Early successional species that are typically dominant on reforestation sites grow rapidly and have extensive root systems that allow high rates of nutrient absorption. For example, a well-developed fireweed (*Epilobium angustifolium* L.) community on a boreal reforestation site contained more than 70 kg ha^{-1} of N in aboveground biomass (Newton and Comeau 1990). Early successional species usually have a rapid turnover of both root and shoot tissue, thus requiring a continuous replenishment of soil nutrients. The rate of nutrient accumulation is tied to their phenological cycle, with high rates of nutrient accumulation occurring during the vegetative growth cycle (Chapin 1983). When these plants die in the fall, the nutrients accumulated in the plants biomass return to the soil. Such plants grow rapidly and respond to site inputs, such as nutrients, with accelerated growth rates, thereby maintaining a short-term competitive advantage.

Late successional species such as spruce normally grow slowly for long periods on sites with low nutrient availability (Section 1.5.2). Thus, when site nutrients become available, late successional species accumulate nutrient reserves rather than have an initial increase in their growth rate (Chapin 1983). Spruce seedlings accumulate nutrient reserves during the latter half of the growing season so that the initial growth during the growing season is dependent upon the reallocation of internal nutrient reserves rather than the absorption of nutrients from the soil (Section 3.6.1). In addition, forest disturbance changes the available nitrogen source from predominantly NH_4^+ to NO_3^- (Section 1.5.2), and spruce species, in general, discriminate against the uptake of NO_3^- and preferentially use NH_4^+ as a main source of nitrogen (Section 3.6.1). This is another factor that limits the ability of spruce seedlings to be competitive on reforestation sites (Kronzucker et al. 1997).

In disturbed ecosystems, the time of peak nutrient availability usually occurs in the spring (reviewed by Chapin 1983). The spring nutrient pulse is more effectively exploited by perennial vegetative species because of seasonal growth strategy, compared with the seasonal nutrient acquisition pattern of spruce species. As a result, spruce seedlings planted on reforestation sites are initially at a competitive disadvantage with the initial nutrient availability cycles of a disturbed ecosystem. As succession proceeds, seasonal patterns of nutrient absorption become less dependent upon plant phenology and more dependent upon seasonal patterns of nutrient availability in the soil (Chapin 1983). As a result, the low annual requirement for nutrients by spruce eventually allows the spruce to gain a competitive advantage over early successional species that are vulnerable to low nutrient availability typically found in more stable northern latitude forest ecosystems (Section 1.5.2).

Vegetation on boreal reforestation sites has a direct effect on nutrient acquisition and growth of spruce seedlings (Munson and Timmer 1989*a*). For example, Norway spruce seedlings had the highest N concentration after planting into 1-year-old clear-cuts having minimal vegetation, while N concentration declined in seedlings when they were planted into older clear-cuts (i.e., clear-cuts of up to 4 years in age) having greater competing vegetation (Bergquist and Örlander 1998). Thus, the control of vegetative competition can increase the available site nutrients to planted spruce seedlings. Foliage nutrient concentrations of newly planted spruce seedlings are enhanced by vegetation control (Sutton 1975; Brand and Janas 1988; Brand 1990; Messier and Kimmins 1991; Munson et al. 1993; Örlander et al. 1996; Jäderlund et al. 1997; Malik and Timmer 1998). Higher nutrient concentrations (i.e., N and P) lead to greater photosynthetic capacity and growth in spruce seedlings (Sections 3.6.2 and 3.6.3, respectively). The improved foliage nutrient concentration of newly planted spruce seedlings results in improved growth, with the positive influence occurring in the first (Malik and Timmer 1998) or second (Brand 1990) growing season. The effects of improved growth for white spruce seedlings was still evident 4 years after application of vegetation control treatments, and this was, in part, attributable to greater levels of N in the current foliage of seedlings receiving the vegetation control treatment (Munson et al. 1993).

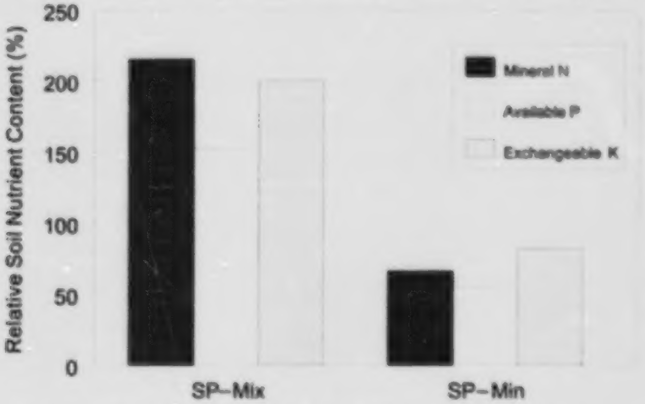
In northern latitude forests, surface organic layers are the main source of available nutrients in the forest soils (Section 1.5.2). Site preparation treatments used to control vegetation influence the fertility of the site. Caution must be taken with the use of site preparation procedures because even modest site preparation can redistribute nutrients to the detriment of planted stock (Sutton 1979). The following are a series of examples where site preparation treatments have altered the fertility of northern latitude reforestation sites.

Site preparation treatments that reduce vegetative competition but leave the organic layers on the forest site cause a gradual release of nutrients (Chapin 1983). This practice can result in little increase in available nutrients for up to 2 years after application of the treatment (Simpson et al. 1997). On the other hand, herbicide application can limit competition on a boreal reforestation site and improve N content and subsequent growth of Norway spruce seedlings (Nilsson et al. 1996). In another example, herbicide application to a clear-cut boreal mixedwood forest resulted in little change in the total nutrient pool of the soil profile over a 6-year period, although the concentration of N was higher while P, K, and S were up to 25% lower in the surface organic horizons (Maynard 1997). The potential loss of nutrients from the site was minimal due to the herbicide treatment, although subsequent nutrient availability within the soil profile is variable between reforestation sites.

Treatments that mix the organic and mineral soil layers (e.g., berms or mounds) increase mineralization within the soil profile (Vitousek 1983; Örlander et al. 1990). This mineralization of the soil after site preparation improves the availability of nutrients for at least 3 years, although the duration of the effect is dependent upon climate and soil conditions (reviewed by Örlander et al. 1990). In the subboreal spruce zone, a mechanical site preparation treatment that mixed the soil horizons increased the soil availability of N, P, and K 2 years after treatment application (Fig. 5.5.4*a*). Mechanical site preparation treatments that retained surface organic layers within the planting spot resulted in increased Norway spruce seedling growth over periods ranging from 3 (Hallsby 1995) to 10 years (Örlander et al. 1997). These examples indicate that the nutrient resources within the surface organic layers ensure that spruce seedlings have adequate nutrients for establishment on reforestation sites.

Site preparation that removes much of the biologically active, nutrient-rich organic layers can reduce site nutrients. For example, removal of the upper soil surface layers through windrowing caused N losses of as much as 750–835 kg N ha^{-1},

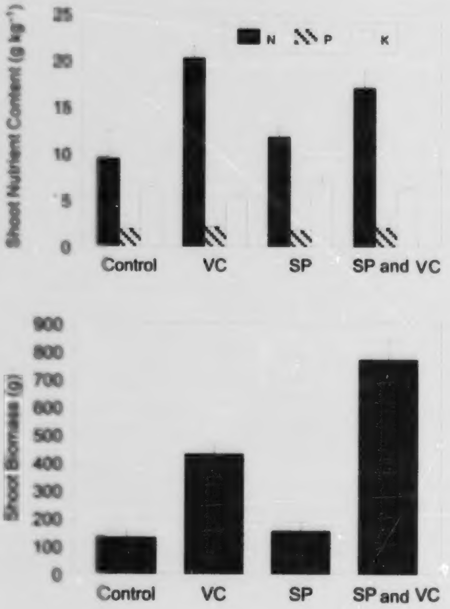
Fig. 5.5.4*a*. The effects of site preparation (SP) treatments (i.e., Mix, intermixed mineral and organic material in a berm; Min, mineral soil in a trench) on nutrient content of the soil on a boreal reforestation site in the north-central interior of British Columbia (55° N lat.) (adapted from Yole and Kranabetter 1996*b*). Soil properties were tested 2 years after application of site preparation treatments, with the control treatment (i.e., representing 100% value) having 37% vegetation cover with mineral N at 17.7 ppm, available P at 25.2 ppm, and exchangeable K at 0.22 mequiv. 100 g^{-1}.



with an additional loss of 150–250 kg N ha^{-1} from the rooting zone resulting from deep plowing on windrowed sites (Foster and Morrison 1987). On a site in the subboreal spruce zone, mechanical site preparation treatments that removed the soil surface organic layer decreased the availability of N, P, and K (Fig. 5.5.4*a*). Blade scarification was associated with the lowest concentrations of foliar P and K in white spruce seedlings 3 years after planting (MacDonald et al. 1998). In addition, blade scarification reduced soil C and nutrient capital in the remaining soil profile by two- to threefold 7 years after the site preparation treatment, which affected long-term performance of white spruce (Burgess et al. 1995). Fire as a means of vegetation control is unique in that it removes the surface organic horizons yet causes a very rapid increase in the available site nutrient reserves just after burning (Chapin 1983; Rapp 1983). However, this increase in available site nutrients after fire is only temporary, as these released nutrients may be readily leached out of the soil (Chapin 1983; Rapp 1983).

Site preparation treatments that remove competing vegetation and alter the surface organic layers of northern latitude forest soils may, or may not, affect the long-term productivity of the forest plantation. Four years after application of vegetation control on a boreal reforestation site, white spruce seedlings had higher N, resulting in greater seedling growth (Fig. 5.5.4*b*). However, there was also a 20% reduction of C and a 28% decrease in N in the forest soil humus (Munson et al. 1993). This type of decrease in C and N in soils is typical of disturbed forest systems where the surface organic layers undergo rapid mineralization after forest disturbance (Bormann and Likens 1979). The reduction of site organic matter and total N represents a rapid mineralization of site reserves and benefits the short-term growth of the forest plantation, although the long-term

Fig. 5.5.4b. Impact of site preparation (i.e., leaving forest humus and logging debris on site but reduced in depth (Control); mineral soil after blade scarification (SP)) and (or) vegetation control (VC) (i.e., herbicide each spring in each of the 4 years following planting) on nutrient content and shoot biomass of white spruce seedlings after 4 years of growth on a boreal reforestation site in central Ontario (46° N lat.) (adapted from Munson et al. 1993).



impacts of this process on stand productivity may not be evident for many years. In contrast, the use of mechanical site preparation has been associated with reduced total soil N (Schmidt et al. 1996), although there was no effect of mechanical site preparation on the foliar N content and growth of white spruce seedlings after 3 years (MacDonald et al. 1998). Munson and Timmer (1995) speculate that the limiting environmental conditions of northern latitude reforestation sites may, in some instances, restrict the response of seedlings to the altered nutrient conditions created by site preparation. Thus, the availability of site nutrient reserves to spruce seedlings can be altered by site preparation treatments, although the magnitude of the growth response is also tied to how these treatments influence other environmental parameters that are known to limit spruce seedling performance (i.e., Section 5.5.1: Light; Section 5.5.2: Temperature; Section 5.5.3: Soil water).

5.5.5 Influence of herbicides on spruce seedling performance

Herbicides are used in plantations of newly planted conifer seedlings to release them from competition. The advantages of herbicides as an effective tool in vegetation management have long been recognized for use on northern latitude reforestation sites because of low cost, ease of use on a wide range of sites, and effective control of resprouting vegetation (Sutton 1970; Otchere-Boateng and Herring 1990). The primary use of herbicides in forestry in Canada is to release plantations from competition (i.e., 85%), while site preparation represents only a small portion (i.e., 15%) of total forestry herbicide use (Campbell 1990). The effectiveness of herbicides is often limited by their ability to selectively damage the competing vegetation without damaging the conifer seedlings. This limits the flexibility and effectiveness of herbicide use. It is beyond the scope of this discussion to examine the physiological effects of specific herbicides on the performance of plants. Information on this topic can be found elsewhere (e.g., Fedtke 1982; Duke 1985). Rather, discussion of this topic briefly addresses how the physiological performance of conifer seedlings is influenced by the application of herbicides. This information can provide an understanding of when best to use herbicides.

There are two general types of chemically synthesized herbicides (Nelson and Haissig 1986). First, there are herbicides that require specific specialized tissue to be present for activity; the predominant version are photosynthetic inhibitors. Some herbicides that are photosynthetic inhibitors are the triazines, substituted ureas, and bipridiliums. Second, there are herbicides that affect a cellular function or functions in any plant cell. Herbicides that have universal effects on cellular function include 2,4-dichlorophenoxyacetic acid (2,4-D), picloram, glyphosate, and amitrole. The primary mode of action of a herbicide is important in understanding the effect it can have on conifer seedling performance and how to manage these herbicide stress effects.

The damage herbicides inflict on conifer seedlings can range from slight alterations in physiological processes, which influence subsequent growth, to tree mortality. For example, sublethal herbicide doses can depress P_n (e.g., triazines: Miroslavova et al. 1983), while stimulating the respiration rates (e.g., 2,4,5-T: Tonecki 1975; triazines: Miroslavova et al. 1983), of Norway spruce seedlings. The extent of herbicide damage is attributed, in part, to the specific chemical, the amount of chemical applied, and the method of application. In addition, the extent of injury to conifer seedlings is due to the interaction of the herbicide with the physiological state of the seedling and the reforestation site environment.

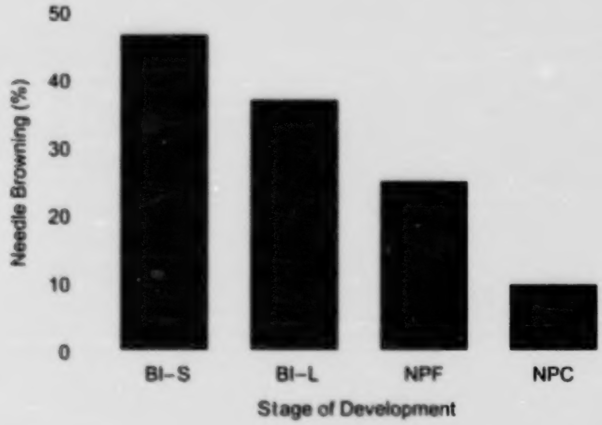
In some cases, reduced performance of the crop species due to herbicide application can be seen, while other times the herbicidal stress is overridden by the positive effects of vegetation control on seedling growth (Sutton 1970). There are numerous studies that have found improved spruce seedling growth over a number of years following the application of herbicides in northern latitude forest plantations (e.g., Sutton 1975; Brand and Janas 1988; Wood et al. 1990; Wood and von Althen 1993; LePage and Coates 1994; Nilsson and Örlander 1995; Fleming and Wood 1996; Reynolds and Roden 1996; Groot et al. 1997; Whitehead and Harper 1998; Cole et al. 1999). Thus, even though herbicides can cause short-term damage to conifer seedlings, benefits to long-term plantation performance must be considered when making the decision whether to use this silvicultural option.

In forest regeneration programs, the time of year that herbicides are applied is important because application is necessary when conifer seedlings are not responsive to the chemical, and weed populations are affected by the herbicide. Optimum timing of herbicide application for effective vegetation control is late spring to early summer, when the competing plants are actively growing (Otchere-Boateng and Herring 1990). However, this is also the period in the growing season when conifer seedlings are most susceptible to these herbicides. A number of studies have reported that late summer and early October are the best times to apply herbicides to forest plantations and have a minimal effect on planted conifer seedlings (Gratkowski 1977; Radosevich et al. 1980). This is also observed in Norway spruce seedlings (Lund-Høie 1975). Lawrie and Clay (1994) found Sitka spruce seedlings had the greatest damage from herbicides during July, with less damage occurring during the spring and fall. The avoidance of herbicide effects has been attributed, in part, to the phenological cycle of the conifer seedlings at the time of application. Spruce seedlings have stopped growth, are going through the early stages of dormancy, and are developing increased stress resistance during the late summer and early fall (Section 3.9). This overall phenological state may be sufficient to allow spruce seedlings to avoid most of the negative effects of herbicides.

Conifer seedling ability to avoid the effects of herbicides in the fall can also be attributed, in part, to the development of the needle cuticle and epicuticular waxes. It is believed that cuticular development prevents penetration of the herbicide from exterior surface into the needle tissue (Radosevich et al. 1980), which may partially explain why actively growing shoots of conifers are more susceptible to herbicides (Zwiazek and Blake 1990*b*). This phenomenon can be seen in black spruce seedlings sprayed with a herbicide over a series of phenological development stages (Fig. 5.5.5). Black spruce seedlings with nonlignified stems and only the initial stages of bud development had the greatest damage to herbicide application, with continued stem lignification and bud development reducing the amount of herbicide damage. Colombo and associates (1998) attributed the development of a resistance to herbicides to a development of needle waxes, which conferred avoidance to herbicide uptake. Lund-Høie (1976) also indicated that cuticle development was also part of the reason for the limited uptake of herbicides in the fall in Norway spruce seedlings. Complete development of the needle cuticle and epicuticular waxes in spruce seedlings can take a minimum of 3 months from the time of budburst (Section 2.2). Since budbreak normally occurs during May and budset occurs in early August for spruce (Section 2.6.1), the development of the needle cuticle and epicuticular waxes would probably be adequate by late summer and early fall to limit the foliar uptake of herbicides.

Conifer seedlings are damaged by herbicide applications during the summer, when they are actively growing, have a low level of seedling water stress, and the rate of photosynthetic activity is high (Radosevich et al. 1980). This is due to the fact that herbicide tolerance is very low when there is a rapid uptake of the

Fig. 5.5.5. Needle browning of black spruce seedlings sprayed with a herbicide (glyphosate at 2 kg acid equiv. ha^{-1}) during different stages of phenological development: (*i*) at budscale initiation (BI), with stem tissue classified as being either green and succulent (S) or brown and lignified (L); (*ii*) early in the process of needle primordia formation in the terminal buds (NPF); and (*iii*) near the completion of needle primordia formation in the terminal buds (NPC) (adapted from Colombo et al. 1998).



herbicide into the plant, and the plants are in a high state of metabolic activity (Nelson and Haissig 1986). Lund-Høie (1983) found Norway spruce seedlings had greater herbicide damage under higher temperatures. This greater herbicide damage was attributed, in part, to higher metabolic activity related to growth and due to the herbicide being translocated to the shoots through passive translocation via the xylem during the movement of water through the seedlings (Lund-Høie 1976). Herbicide damage in pine seedlings is reduced as the level of seedling water stress increases during the time of herbicide application (Paley and Radosevich 1984). This is due to the fact that as seedlings undergo water stress, their stomata close (Section 3.5.2.1), and water movement through the seedling is reduced (Section 2.1.2). Thus, water stress limits the passive translocation of herbicides through the xylem, thereby limiting the concentration of the herbicide in needle tissue.

An alternative approach recommended by Reynolds and Roden (1996) was to treat the site with herbicide in the spring and delay planting by 1 year. This was found to provide the optimal treatment for maximum survival and growth of black spruce seedlings during plantation establishment, as herbicide residues rapidly dissipate and degrade in the natural environment (Reynolds and Roden 1996). In another example, 1 year after application of glyphosate to reforestation sites where Sitka spruce was planted, remaining residue was strongly adsorbed to organic matter, soil particles, and (or) stream bottom sediments where they appeared to be inactive and immobilized (Reynolds et al. 1993). Also, it appears that the remaining residues retained in the soil from standard herbicide applications used in vegetation management programs do not pose a permanent risk to normal soil microbiological processes (Kimmins 1975). This herbicide application approach can have long-term benefits on spruce plantation performance. For example, a white spruce plantation treated with herbicides in the summer prior to planting had growth that was ~3.5 times greater than a plantation not treated with herbicide, measured 12 years after treatment (Harper et al. 1997). This delayed planting approach removes the chance of direct exposure of the spruce seedlings to the deleterious effects of herbicide application.

An alternative group of herbicides are now being tested for application within silvicultural programs. These are microbially produced herbicides (e.g., bialaphos) which have been shown to inhibit photosynthesis and eventually cause death of the plant tissue (Tachibana et al. 1986*a*, 1986*b*). Recently, this type of herbicide was assessed for its effect on the performance of spruce species. Application of bialaphos to actively growing white spruce seedlings resulted in the development of chlorotic needles and a reduction in P_n (Sy et al. 1994*b*). Survival rates were high for spruce seedlings treated with bialaphos, although subsequent growth was affected by timing of application (Sy et al. 1994*a*). Tolerance of spruce to bialaphos was lowest when applied in July and highest in August, with low tolerance resulting in greater development of chlorotic needles and a reduction in subsequent growth, while high tolerance resulted in no long-term influence on subsequent growth (Sy et al. 1994*a*). Interestingly, it was found that the percentage of cuticular wax on current-year needles was positively correlated to the growth rate of treated seedlings. This relates back to the earlier discussion that greater cuticle development can limit the foliar uptake of herbicides by conifer seedlings. Sy et al. (1994*a*) concluded that because bialaphos has a strong effect on species that compete with spruce seedlings, this microbially produced herbicide is a potential alternative to chemically synthesized herbicides for vegetation management in conifer plantations.

The effect of herbicides on conifer seedlings is due to the interaction of the herbicide with the physiological state of the seedling and the reforestation site environment. Currently, there is limited information related to the effects of herbicides on the physiological performance of spruce seedlings. Available information seems to indicate that herbicides can have the lowest level of effect on the physiological activity of spruce seedlings when this silvicultural treatment is applied in late summer or early fall. At that time, spruce seedlings have no shoot growth occurring, the cuticle of the needles is fairly well developed, and seedlings have developed a level of stress resistance as they start to enter the initial stages of dormancy. If herbicide treatments have to be applied in late summer, a period of cool–dry environmental conditions minimizes the negative effects of herbicides on spruce seedling performance.

5.6 Silvicultural systems that provide partial forest canopy retention

Manipulation of the forest stand structure by harvesting either all (clearcutting) or a portion of the stand (canopy retention silvicultural systems) is an ecologically based method for the regeneration of selected tree species (Daniel et al. 1979). Clear-cutting is a method where open site conditions are dominant and forest edges are minimized. As a result, regeneration occurs without dependence on the protection of the border forest structure. The prime objective of clear-cutting is to reestablish an even-aged stand by removing the mature forest overstory, thereby promoting an early successional stand from the creation of a high-light environment. Since clear-cutting is the primary silvicultural system used in regenerating northern latitude spruce forests, most of the previous discussion has pertained to the regeneration practices associated with this silvicultural system. Silvicultural systems that retain a partial forest canopy are currently being considered as a potential alternative for establishing spruce plantations. This section briefly discusses the merits of a number of partial forest canopy retention systems as alternatives to clear-cutting. The discussion focuses on the environmental changes and the subsequent performance of spruce seedlings that occur with the use of these partial forest canopy retention systems.

Shelterwood systems are used to promote regeneration of the future stand under the shade and protection of an overstory forest structure. This is an approach where a young stand of trees is established under a forest canopy with the intent to provide some characteristics of the original stand structure (Matthews 1989). This is accomplished by leaving standing dead trees and retaining some live trees within the forest canopy over the rotation through limited harvesting of the overstory canopy. The intent of this silvicultural system is to provide stand regeneration through natural seeding from trees within the forest canopy rather than from the artificial regeneration approach normally used with the clear-cutting system (Matthews 1989). Weetman (1996) contends that, of all the classical silvicultural systems, some form of the shelterwood system has the best potential for use within overmature Canadian conifer ecosystems.

Shelterwood systems can be considered in two forms. A uniform shelterwood system is used to produce uniform openings in the forest canopy that allow for the regeneration of a new forest in an even-aged manner (Matthews 1989). An irregular shelterwood system produces an uneven-aged stand through a series of successive regeneration harvests, resulting in a long and indefinite regeneration period (Matthews 1989). This silvicultural system allows for the manipulation of stand density to create site environmental conditions that are preferred by the intended crop species, making the shelterwood system the most flexible way of regenerating a stand.

Selection systems create small canopy gaps by the removal of single or small groups of trees throughout the forest (Matthews 1989). These overstory removal treatments can be used to tailor light environments to the shade tolerance of the target species. A selection system has two primary characteristics: (*i*) stands are always uneven-aged, and (*ii*) the regenerating stand never loses protection of the mature forest overstory. Within the group selection system, trees are felled in groups in order to create gaps of sufficient size to enable natural regeneration. Group selection is a possible alternative that can produce abundant natural spruce regeneration if the small forest openings are no larger than ~0.3 ha in size (Zasada and Argyle 1983; Matthews 1989).

Strip-cutting is a system whereby the forest is harvested in narrow strips, with the mature forest retained around these strip-cuts (Matthews 1989). This silvicultural system is applied as narrow strip-cuts that alternate with leave strips; the leave strips provide a seed source for the cut areas (Matthews 1989). Matthews (1989) states that this system is really nothing more than clear-cutting, unless the width of the cut strips are less than half the height of the trees left in the adjoining forest stand. This system is intended to produce uniform openings in the forest canopy that can allow for the regeneration of a new forest in an even-aged manner.

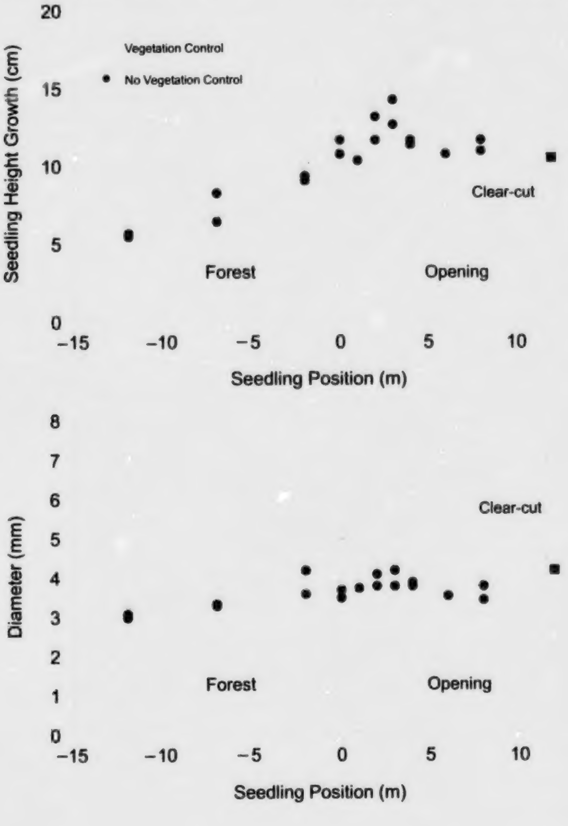
Partial forest canopy retention systems create forest edges which produce a range of microclimates into which spruce seedlings are planted. Depending upon the orientation of the forest edge, seedlings are exposed to a range of light, air and soil temperatures, humidity, soil water, and soil nutrient availability. There are two types of climates that can occur along the forest edge (Geiger 1980). First, there is a transitional climate from within the inner edge of the forest out into the opening. Second, the edge of the forest forms a step in topography, which shelters the opening from incoming light and wind. As the opening increases in size, there is a diminishing effect of the adjacent forest on the microclimate of the opening. This is why Matthews (1989) argues that if these openings in the forest canopy are small enough, the remaining forest stand can provide a microclimate within the cut area that is comparable to the forest stand. The choice of silvicultural system and specific residual canopy density create forest edges. Thus, partial forest canopy retention systems can create a multidimensional array of environmental conditions when considering how planted spruce seedlings are going to respond to the site. Available information on the effects of forest edges created from the use of canopy retention silvicultural systems are incorporated into the following discussion.

The choice of silvicultural system and the specific residual canopy density are dependent on site type, reliance on natural or artificial regeneration, the silvics and regeneration strategy of the target species, and specific management objectives. The practicality of using some of these partial forest canopy retention systems in context with the development of spruce plantations needs to be determined. This section presents a number of examples of the manner in which silvicultural systems that provide partial forest canopy retention can influence the ecophysiology of planted spruce seedlings.

The use of partial forest canopy retention systems within northern latitude forests creates a forest canopy structure with tree species composition ranging from only conifers to a mixed-wood canopy or only hardwoods. In this discussion, the actual composition of the canopy is of secondary importance. It is primarily important to recognize that partial forest canopy retention systems can influence the microclimate at the location where spruce seedlings are planted. Studies have found that spruce seedlings have improved growth (Tanner et al.

1996; Man and Lieffers 1999), while numerous studies have found that spruce seedlings had limited growth (Hagner 1962; Youngblood and Zasada 1991; Kabzems and Lousier 1992) (Fig. 5.6*a*) within these partial forest canopy retention systems when compared to seedlings planted in adjacent clear-cut sites. Spruce seedling performance is affected by site environmental factors such as light level, air and soil temperatures, humidity, soil water, and soil nutrient availability (Section 3). The availability of these site resources also affects the development of vegetation competition, which in turn influences the performance of

Fig. 5.6*a*. Second growing season height growth and diameter of planted white spruce seedlings with and without vegetation control, spanning from within a hardwood partial forest canopy retention system (basal area of 36 m^2 ha^{-1}) into a strip clear-cut on a northern latitude site (Chapleau, Ont., 47° N lat.) (adapted from Groot et al. 1997 and Groot 1999). Negative distances are located within the forest stand, and positive distances are located within strip-cuts. The regression equations are as follows. For height growth: vegetation control: $y = 5.34 + 14.59/(1 + e^{-(x-0.46)/3.03})$, $r^2 = 0.96$; no vegetation control: $y = 6.22 + 5.53/(1 + e^{-(x+1.92)/1.07})$, $r^2 = 0.81$. For diameter: vegetation control: $y = 3.12 + 3.54/(1 + e^{-(x-0.053)/1.83})$, $r^2 = 0.97$; no vegetation control: $y = 3.05 + 0.65/(1 + e^{-(x+6.71)/0.36})$, $r^2 = 0.40$.The open and filled squares (with and without vegetation control, respectively) represent seedlings grown in an adjacent clear-cut.



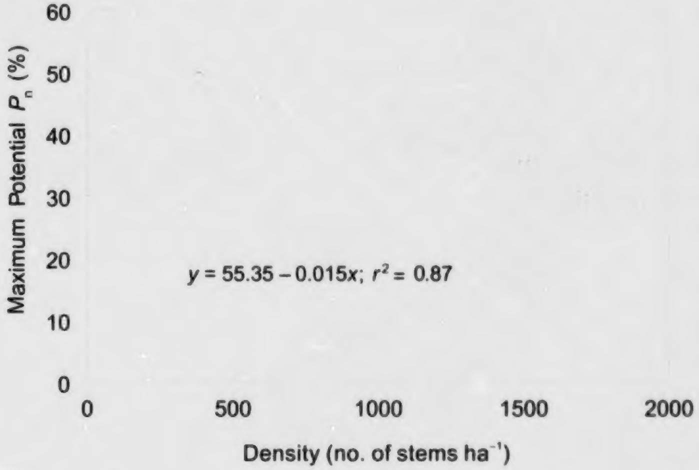
spruce seedlings (Section 5.5). Thus, the use of partial forest canopy retention systems can alter the seedling environment in many ways, making it difficult to ascribe any single environmental variable as the sole factor affecting spruce seedling performance. With this caveat noted, the following discussion presents examples that show the effects of partial forest canopy retention systems on each of the above environmental factors, and where information is available, the influence on the performance of planted spruce seedlings.

The structure and species composition of the forest canopy influence the amount of light reaching spruce seedlings (Section 1.1.2). The following are a series of examples of how various partial forest canopy retention systems can influence the amount of light penetrating the canopy and reaching spruce seedlings. First, in a mature coniferous boreal forest with a well-developed forest canopy (i.e., 436 stems ha^{-1}, basal area of 46 m^2 ha^{-1}), only 11% full sunlight reached beneath the forest canopy, with only 4% full sunlight reaching the forest floor (Jull et al. 1997). After application of a shelterwood system, the forest canopy was reduced (i.e., 100 stems ha^{-1}, basal area of 19 m^2 ha^{-1}), which allowed 61% full sunlight to penetrate beneath the forest canopy, with 36% full sunlight reaching the forest floor. Second, group selection, irregular shelterwood, and single-tree silvicultural systems that removed an actual basal area of 66, 50, and 45%, respectively, of a mature coniferous boreal forest allowed 40, 44, and 31% full sunlight, respectively, to penetrate through the forest canopy (Jull et al. 1996). These examples show that as the density of stems per a given area decreases within the partial forest canopy retention system, the light reaching spruce seedlings increases. Changes in the density of the forest canopy can affect the photosynthetic process of spruce seedlings by determining where light is captured within the forest (Fig. 5.6*b*). Spruce species have a decrease in P_n and growth as light is reduced (Sections 3.1 and 5.5.1), and light levels have a direct effect on spruce species shoot system structure (Section 2.6.1.3). These examples show that the density of a partial forest canopy retention system can affect light reaching the forest floor, thereby influencing the potential photosynthetic capacity and subsequent growth of spruce seedlings throughout the growing season.

Small group selection and strip-cutting are silvicultural systems that can also alter light transmission to spruce seedlings. Removal of the forest canopy through use of these silvicultural systems can provide a high-light environment (Berry 1964). For example, small group selections provided 55 and 26% of total growing season solar radiation in 18- and 9-m circles, respectively, while strip-cuts provided 68 and 57% of total growing season solar radiation in 18- and 9-m strips, respectively, compared to 18% for an undisturbed forest (Groot et al. 1997). These findings indicate that the creation of gaps in the forest canopy allows for the penetration of light to the ground surface in sufficient quantities to ensure the development of spruce seedlings.

Light received at the forest floor is also dependent upon the location within the forest gap and along the forest edge in relation to the sun. Geiger (1980) notes

Fig. 5.6*b*. The percent of maximum net photosynthesis (P_n) of white spruce seedlings in relation to the light penetrating through a partial hardwood canopy retention system at various levels of stand density (adapted from Tanner et al. 1996). Percent of maximum net photosynthesis (P_n) was determined by measuring light reaching the forest floor through the hardwood canopy during the growing season in relation to the photosynthetic capacity of spruce seedlings at a given light level (i.e., photosynthetic capacity is based on a generalized curve for P_n in relation to photosynthetically active radiation, similar to Fig. 3.1*a*).



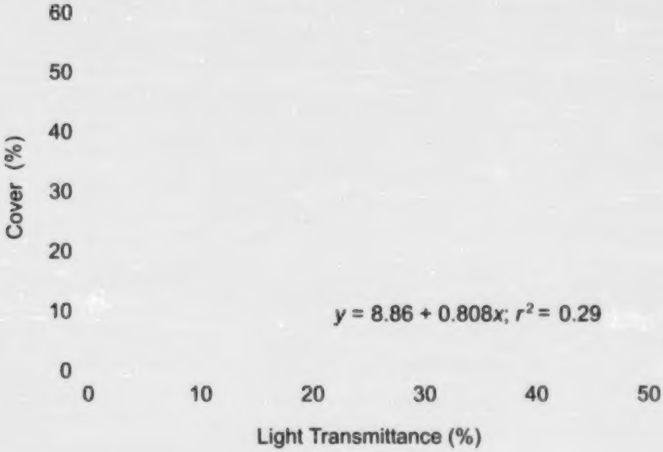
that, in general, for northern latitude forests, there is a symmetry between the east and west edges in their exposure to direct sunlight. In contrast, the forest edge with a southern exposure receives the most and the northern exposure the least sunlight, with the northern exposure having reduced direct sunlight in the summer and deprived of direct sunlight during the winter (Geiger 1980; Canham et al. 1990). For example, during late spring and early summer, the northern exposure locations within an 18-m strip-cut received only 40% of available solar radiation, while the southern exposure locations received over 70% of available solar radiation (Groot et al. 1997). Strip-cuts orientated east to west result in light levels under the crowns of residual trees in the forest edge that are comparable to the strip opening (Canham 1988). Shelterwood systems with an east to west orientation can also result in light penetration into the understory along the south-facing cut-face (Matthews 1989). However, these light levels along the forest edge decrease quite rapidly to closed forest canopy light levels after moving just 10 m into the forest (Groot et al. 1997). These findings indicate that silvicultural systems that provide gaps and edges in the forest canopy can alter the light environment at the forest floor.

The amount of light that reaches spruce seedlings growing under a partial forest canopy retention system differs, depending upon the species make-up of the forest canopy. A forest canopy made up of deciduous species, compared to conifer species, has a different light transmission pattern which is dependent upon the seasonal developmental stage of the canopy (Section 1.1.2). For example, the amount of full sunlight that reached the forest floor in the spring and summer, respectively, was 59 and 26% in a pure hardwood stand compared to 22 and 8% in a mixed-wood stand; light was very low under both forest canopies in the summer (Constabel and Lieffers 1996). Also, light transmission through hardwood canopies increases in the fall after leaves have dropped (Section 1.1.2). Spruce seedlings in the understory can take advantage of these seasonal periods of high light transmission through the leafless hardwood canopy by quickly regaining photosynthetic capacity in the spring and maintaining photosynthesis into the fall (Man and Lieffers 1997*b*). On the other hand, light transmission through a conifer stand during the growing season is primarily dictated by stand basal area. Thus, the ability of spruce seedlings to photosynthesize in the understory of a conifer forest can only occur if the stand density is low enough to allow light penetration or through the occurrence of sun flecks (Sections 1.1.2 and 3.1). It is important to recognize that the light reaching spruce seedlings through a partial forest canopy retention system is related to the density as well as composition of the forest canopy.

As light penetrates into a partial forest canopy retention system, it can be intercepted by the overstory, shrub layer, or herb layer before it reaches the forest floor. Depending upon the density of the overstory forest canopy, these partial forest canopy retention systems can alter the amount of competition that develops over time from shrubs, grasses, and forbs. The implementation of a partial forest canopy retention system can disturb the forest floor and initially reduce the competition level around planted spruce seedlings (Youngblood and Zasada 1991; Kabzems and Lousier 1992; Tanner et al. 1996), although within a couple of years after disturbance, the understory vegetation can develop quite rapidly (Groot et al. 1997).

The density of a partial forest canopy retention system has a direct effect on light transmission to the understory vegetation. If the canopy is opened up enough to allow sufficient light transmission to the forest floor, then understory vegetation can develop, and the forest structure changes over time. For example, in older boreal forested stands with a range of overstory canopy densities, greater light was transmitted below the forest canopy as the density of the forest canopy was reduced, which in turn increased the development of shrubs (Fig. 5.6*c*). In temperate forests, understory vegetation is eliminated when the forest canopy intercepts greater than 80% of incoming light, with greater light transmission resulting in greater understory vegetation development (Hill 1970). When the percent cover of the understory vegetation increases, there is a decrease in the proportion of light transmitted to the forest floor (Messier et al. 1998). The net effect is that changing the forest structure to bring more light through the forest canopy alters the layer of vegetation that actually intercepts light before it reaches the forest floor. Greater light transmission to the forest floor can eventually alter the structure of the forest stand by stimulating the development of

Fig. 5.6c. Average cover of shrubs less than 1.3 m in height in relation to overstory light transmission across a series of sites with varying degrees of a partial hardwood canopy retention system in the boreal forest in west-central Alberta (54° N lat.) (adapted from Lieffers and Stadt 1994).



understory vegetation as well as advanced conifer and hardwood regeneration, which would ultimately produce a multilayered stand (Tappeiner et al. 1997).

There seems to be little difference in the amount of light that reaches spruce seedlings irrespective of the forest canopy density due to the development understory vegetation. For example, only ~6% of incident light reached the forest floor during the summer, because greater light transmission through the overstory resulted in increased light interception by the understory (Constabel and Lieffers 1996). A similar pattern was also reported 2 years after a partial forest canopy removal (Groot et al. 1997). Constabel and Lieffers (1996) concluded that because of the interception of light by the combination of overstory and understory vegetation, seedlings less than 0.5 m in height were at or below the photosynthetic light compensation point for much of the summer. White spruce annual growth, under a mixed-wood forest canopy, only increased as saplings grew in height, presumably because they overtopped successive layers of shading vegetation (Lieffers et al. 1996*b*). Also, spruce seedling growth increases when understory vegetation control is incorporated into the silvicultural practices (Fig. 5.6*a*). It is important to recognize that just like in a clear-cutting system (Section 5.5.1), a partial forest canopy retention system creates conditions favorable for secondary successional species; therefore, competition for available site resources occurs in either system.

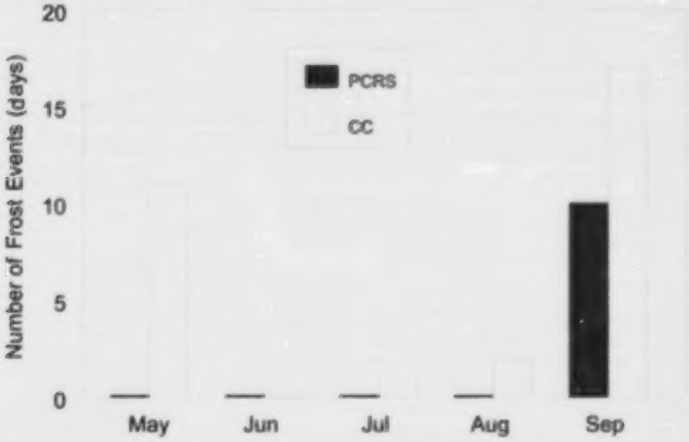
Both air and soil temperatures around newly planted spruce seedlings are altered, depending upon the location of solar radiation absorption on a reforestation site (Section 1.1.2). In a partial forest canopy retention system, the canopy becomes the major location of radiative energy transfer rather than the soil surface around the seedling (Sections 1.2.1–1.2.3) and can have a beneficial or deleterious effect on seedling performance. For example, sites with a partial forest canopy retention system can have lower growing season temperatures when compared to adjacent clear-cut sites (Kabzems and Lousier 1992; Marsden et al. 1996; Groot et al. 1997; Jull et al. 1997). This corroborates what is known to occur with vegetation competition on clear-cut reforestation sites where increased competition causes a reduction in the soil temperature during the growing season on northern latitude reforestation sites (Section 5.5.2).

In northern latitude forests during midsummer, there is a general pattern of the east- and west-facing, not the south-facing, forest edges receiving the greatest amount of heat. The south-facing forest edge receives the greatest amount of heat about the time of the equinoxes (Geiger 1980). The forest edge with a northern exposure receives the lowest amount of heat during the summer. This was reflected in the lower average summer soil temperatures (at 5 cm) that were recorded in northern (14°C), compared to southern (19°C), exposure locations within an 18-m strip-cut (Groot et al. 1997). Growing season temperatures can vary across the forest opening and along forest edges created by partial forest canopy retention systems. This can create a wide array of temperature microclimates in which to plant spruce seedlings.

In certain situations, a partial forest canopy retention system may cause low growing season temperatures that can limit spruce seedling performance. Northern latitude reforestation sites can have low soil temperatures throughout the growing season, and the presence of vegetation cover can cause a further reduction in soil temperatures (Sections 1.2.1 and 5.5.2). Low soil temperatures can influence water movement through seedlings (Section 3.5.1). In addition, spruce seedling gas exchange capacity (Section 3.5.1), the ability to take up nutrients (Section 3.6.1), and subsequent growth (Section 3.5.1) are all limited as soil temperatures decrease. Partial forest canopy retention systems can alter soil temperatures of the reforestation site which have a direct influence on the physiological response and morphological development of spruce seedlings.

A partial forest canopy retention system can reduce the potential for spring and summer radiation frosts. The number and severity of frosts is reduced on sites where a partial hardwood canopy is retained (Tanner et al. 1996; Groot et al. 1997) (Fig. 5.6*d*) because a tall forest canopy reduces the net radiative loss from the ground surface (Sections 1.2.1 and 1.2.3). A partial forest canopy can increase air temperatures by up to 4°C on the coldest springtime nights (Geiger 1980). In another example, where the conifer overstory of a northern latitude forest was retained at 50% of nonharvested canopy cover, there were only 3 frosts below –3°C between June 1st and September 1st compared to 33 frosts in an adjacent clear-cut (Stathers 1989). On northern latitude reforestation sites, the potential for summer frost decreases as vegetation cover increases (Section 5.4.3). Radiative frosts can cause physiological stress in spruce seedlings and reduce seedling performance (Sections 3.3.1 and 3.7.4). A number of studies have found that spruce seedlings are less susceptible to summer frost when they are growing under a partial forest canopy retention system compared to an open

Fig. 5.6*d*. The number of frosts that occurred throughout the growing season on both a clear-cut site (CC) and a partial hardwood canopy retention system (PCRS) boreal site (northern British Columbia, 59° N lat.) (adapted from Kabzems and Lousier 1992).



reforestation site (Hagner 1962; Leikola and Rikala 1983; Hånell 1992; Groot and Carlson 1996; Groot et al. 1997; Tanner et al. 1996; Man and Lieffers 1999).

Partial forest canopy retention systems can alter the atmospheric demand of the air within the hydrologic cycle of the reforestation site. A forest canopy typically decreases the daytime temperature around seedlings and increases site evapotranspiration which can cause an increase in the relative humidity. Any combination of decreasing air temperature or increasing relative humidity can decrease the VPD (Section 1.3.2). Sites with a partial forest canopy retention system can lower VPD during the growing season (Marsden et al. 1996; Groot et al. 1997; Man and Lieffers 1999). White spruce seedlings in more sheltered environments created by partial forest canopy retention can have greater g_{wv} (Groot et al. 1997) and higher P_n (Man and Lieffers 1999) than seedlings in exposed environments, with this trend related to the change in site VPD. Since spruce species gas exchange capacity is directly affected by changes in the VPD of the air (i.e., greater P_n and g_{wv} under lower VPD, Section 3.2), it seems feasible that partial forest canopy retention systems can create a low VPD environment where greater spruce seedling gas exchange can occur.

Soil water conditions around newly planted spruce seedlings may also be altered by the partial forest canopy retention systems. Alteration of the soil water depends upon the soil texture and structure (Section 1.3.1) and the level of competition from the understory and overstory for water (Section 5.5.3). The forest vegetation structure affects seasonal soil water availability through both evapotranspiration and interception of incoming precipitation (Section 1.3). Thus, it is not surprising that in certain instances partial forest canopy retention systems within northern latitude forests are reported to reduce soil water availability (Kabzems and Lousier 1992; Groot et al. 1997). However, in other instances, they have no effect on soil water availability (Kabzems and Lousier 1992; Marsden et al. 1996; Tanner et al. 1996). Forest edges may also create conditions where there is a range in soil water availability across a partial canopy opening due to the greater heat load during the summer on the south-facing, compared to the north-facing, edges. This was reflected in the lower soil water content recorded during the midsummer in southern, compared to northern, exposure locations within an 18-m strip-cut (Groot et al. 1997). Spruce seedling physiological activity and growth is affected by water stress (Section 3.5.2.1). In all of these reported studies (i.e., Kabzems and Lousier 1992; Tanner et al. 1996; Groot et al. 1997), soil water could be a contributing, but not the primary, environmental factor that limits the performance of underplanted spruce seedlings. Groot and associates (1997) reported that white spruce seedlings never reached Ψ that was considered to be stressful throughout the growing season. In northern latitude forests, the performance of spruce seedlings that are planted under a partial forest canopy may, or may not, be limited by forest vegetation competing for soil water, depending upon the vegetation complex of the site and frequency of precipitation.

Nutrient status of spruce seedlings may be affected when they are planted under a partial forest canopy. In northern latitude forests, N is normally bound up in the forest floor, organic layers, and within the vegetation and is not available to planted spruce seedlings unless through mineralization and nitrification (Section 1.5.2). The increased availability of N only occurs if the soil environment, predominantly soil temperature and water, are optimal. As reported above, seasonal soil temperatures are lower under a partial forest canopy, which can then subsequently influence the availability of N in the soil. Higher N concentrations lead to greater photosynthetic capacity and growth in spruce seedlings (Sections 3.6.2 and 3.6.3, respectively). Partial forest canopy retention systems can have no effect (Kabzems and Lousier 1992) or may reduce (Lieffers et al. 1993) the N content in needles of spruce seedlings. In addition, the form of N available within late successional boreal forest soils is NH_4^+, while the available N source changes predominantly to NO_3^- after harvesting (Section 1.5.2). Hardwood species found in the canopy of some partial forest canopies and competing low-lying vegetation are more effective at taking up both sources of N, while spruce species preferentially use NH_4^+ as their source of N (Section 3.6.1). For example, red (Nadelhoffer et al. 1995) and white (Kronzucker et al. 1997) spruces have lower rates of NO_3^- assimilation in comparison to deciduous species found in mixed-wood forests. It has been proposed that limited growth in planted spruce seedlings is due, in part, to their inability to use the main source of N that is available on disturbed sites (Section 5.4.7). Further work is needed to clarify whether there is a long-term effect of partial forest canopy retention systems on the nutrient dynamics of the site and how this affects the nutrient status and subsequent growth of spruce seedlings.

This section discussed how partial forest canopy retention silvicultural systems can alter the site environmental conditions, which in turn influence the ecophysiological response of spruce seedlings. Currently, there is a limited body of work from which to draw conclusions on whether or not these systems are a viable option for spruce regeneration programs.

5.7 Concluding remarks

In this section, major ecophysiological principles have been examined in relation to spruce seedling performance under silvicultural practices of the forest regeneration process. The intent was to give the reader an appreciation for the ecophysiological response of spruce seedlings as they are influenced by nursery cultural, storage, and handling practices prior to planting and environmental conditions and silvicultural practices after planting on reforestation sites. Foresters need to recognize that nursery cultural and preplanting silvicultural practices can affect the physiological performance, and thus subsequent growth, of spruce seedlings immediately after planting. In addition, spruce seedling performance on a reforestation site is directly related to physiological response to site environmental conditions. Primary site environmental variables, such as light, temperature, water, and nutrient content all influence seedlings. Environmental conditions of the reforestation site can be manipulated by silvicultural practices. Foresters must recognize that their application of field site silvicultural practices has a direct influence on the physiological response and morphological development of spruce seedlings.

It is usually inevitable that spruce seedlings undergo some physiological stress when they are exposed to site environmental conditions and regeneration practices. Foresters require a basic knowledge of the physiological response of spruce seedlings to the reforestation environment. If foresters have this understanding of both primary seedling physiological processes and site environmental conditions, proper forest regeneration planning can be implemented to minimize seedling physiological stress. In this way, forest regeneration decisions based on a sound knowledge of ecophysiological principles can improve the success of spruce seedling survival and growth.

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